Information-theoretic Bounded Rationality: Timing Laws and Cognitive Costs Emerge from Rational Bounds on Information Coding and Transmission

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Dedication

To Emily, Abe, and Oakley.

Abstract

Cognitive models are used to characterize and understand task performance in humans. Human behavior often deviates from predictions made by models that assume perfect rationality. Imposing constraints on cognitive resources, time, and/or information, while still assuming optimal function within those bounds, produces better characterizations of behavior. However, many of the proposed constraints and costs are ad-hoc and are not derived from fundamental limitations on computation.

We suggest that behavioral performance is limited by the necessity of encoding and transmitting information about the world in the brain. Encoding information imposes a set of intrinsic bounds, defined by signal power, noise power, and knowledge of environmental statistics, that can be understood and quantified using concepts from information theory. In this dissertation, we investigate the patterns of behavior that should arise if cognition is subject to these bounds. Using an information transmission mechanism built using stochastic processes and Bayesian inference, we show that known 'laws' of human behavior, including the Hick-Hyman law and the Power Law of Learning, are direct consequences of unavoidable limitations on the efficiency of information transmission.

By instantiating constraints on information transmission in a working system, we are able to quantify transmission costs induced by task performance. This provides a unifying and principled explanation of cognitive costs and mental effort: effort arises in tasks that require expensive information transmission and is reduced through practice as learned task statistics are exploited to improve efficiency. To test the extent to which humans exploit task statistics to improve efficiency, we measured behavior on a version of the N-back task modified to include a predictable structure in target responses. We found that human data closely matches model predictions, suggesting that humans integrate information about both task structure and past images to produce responses. This finding is an experimental validation of our model, and suggests that the N-back task is more complex than is normally assumed. In sum, we show that treating cognition as a process constrained by fundamental bounds on information transmission provides a unified explanation of a wide range of behavioral phenomena.

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Chapter 1

Introduction

Cognitive science is home to almost as many models as phenomena they are intended to describe. This circumstance stands in sharp contrast to the physical sciences, in which scientists strive for and expect simple unifying principles, like Newton's axiomatic laws, from which individual phenomena arise as particular circumstantial manifestations. But where are our first principles, from which we can hope to derive a coherent set of expectations about how cognition *should* operate? In cognitive science, we would call a framework built from axiomatic constraints *normative*, in that it would make a set of predictions about how cognition should operate if, in fact, those constraints hold. Treating cognition as a process operating optimally but within a set of bounds is a well-established idea [1], but the exact nature of the constraints is still a matter of debate.

We adopt the perspective, shared by many [2, 3, 4, 5], that cognitive function is concerned with the storage, maintenance, transfer, and updating of information for the purpose of acting in the world. Cognitive processes and the observable behavior they subserve are therefore bound by the constraints inherent in encoding information about an environment whose properties are only partially known, and transmitting information in the presence of noise. The implementation of these processes in the brain is additionally bound by physical constraints, including the availability and use of energetic resources [6]. In this dissertation, we consider the consequences that these limitations imply with respect to learning, behavior, and effort allocation. As we will show, constraining information encoding and transmission leads to the production of

learning rates and patterns of reaction times that closely match known 'laws' of human behavior. It also predicts how behavior should alter when task statistics change, provides a mechanism for describing which tasks should be effortful, and suggests a principled connection between the experience of effort and the utilization of metabolic resources. In short, we adopt a bounded rationality approach in which bounds emerge from information-theoretic limitations.

In order to connect theoretical constraints to measurable behavior, we introduce a simple, principled model of information transmission that is built using stochastic processes, Bayesian inference, and Shannon entropy. The model, which we call the Bayes-Poisson model, shares certain similarities with a neural rate code, but is intended to serve purely at David Marr's algorithmic level of analysis rather than model physical neurons [7]. Using this model, we are able to reproduce a range of behaviors exhibited by humans, as mentioned above. Several of these relate to reaction times in tasks. For example, the Hick-Hyman law describes a phenomenon in which subject reaction times are linearly related to the entropy of task stimuli [2, 3]. This relationship is captured by the Bayes-Poisson model, which is also able to account for the observation that the Hick-Hyman law only holds after extensive task practice. The model produces log-normal reaction time distributions in which the variance increases with the mean, a phenomenon widely observed in human subjects, and is also able to produce speed-accuracy tradeoff curves. In Chapter 2 we describe the Bayes-Poisson model and its reproduction of human-like patterns of reaction times.

Many of the Bayes-Poisson model's properties follow from its capturing and maintaining the relative probability of messages in a prior distribution predicting the next possible message. The prior acts as information about an upcoming transmission obtained *a priori*, that is, before the observation in question. As a general rule, the prior serves to reduce transmission time and increase transmission efficiency: fewer observations are needed to make a decision, as information about which observations are likely is already captured by the prior. The process of developing a prior on a new task by tracking the relatively frequency distribution of messages results in gradually faster average transmission times. This results in the Power Law of Learning, which we discuss in greater detail in Chapter 3.

When task statistics change, a strong prior can be maladaptive. If a prior is in

sudden conflict with task statistics, the Bayes-Poisson model predicts that transmission times (and error rates) increase. We suggest that this is analogous to the situation in 'cognitive control' tasks, in which conflicting information results in longer reaction times. In commonly-used tasks such as the Stroop and Flanker tasks [8, 9], conflict resides primarily in the stimulus itself: two conflicting messages are transmitted and must be disambiguated in order to construct a response. To more closely investigate the role of compatible and incompatible prior information on response times and error rates, we constructed a modified version of the N-back task, in which we embedded into some stimulus blocks a particular statistical structure in target responses. We found that when structure was present, subjects reacted more quickly and with fewer errors. Conversely, when expectation about task structure was suddenly violated, response times and errors increased. As we describe in Chapter 4, this behavior is closely matched by the Bayes-Poisson model, but only when structural information is encoded into stimulus and response priors.

In Chapter 5, we enumerate the array of tasks that produce subjective feelings of mental effort and fatigue, and suggest that they share a common factor: high information transmission costs. One critical benefit of an instantiated model of information transmission like the Bayes-Poisson model is that it can quantify and measure transmission cost and relate it to properties like channel noise, receiver entropy, and transmission time. In the Bayes-Poisson model, transmission cost is measured by the count of spike events allocated to encoding a signal, driven by a (theoretical) energy allocation rate. Transmissions that take longer are more costly; this is the case in tasks with high stimulus entropy, or new tasks for which a task-optimized prior has not yet been developed. It is also the case with conflicting stimuli or maladaptive priors, as mentioned above. Increasing signal power shortens response times, but at the cost of a higher energy utilization rate; costs co-vary with transmission time, but are not identical to time.

Finally, in Chapter 6, we discuss the feasibility of a relationship between subjective experiences of mental effort and the physical energetic costs of cognitive processes. As we note in Chapter 5, modern accounts of mental effort measure cognitive cost in units that are external to the decision making system: as negative utility [10], for example, or cost-of-control [11]. Treating cognitive costs as opportunity costs [12] turns effort allocation into a constraint in a time- and task-allocation problem, but still does not explain

why subjects nevertheless use heuristics, exploit task structure, and otherwise choose to reduce effort within tasks, even when it has no effect on time-on-task. We discuss the possibility that mental effort is a signal to avoid engagement in tasks that utilize energetic resources without sufficient concurrent reward. Such frugality of resource use only makes sense in a context in which resources are limited. We propose that astrocytic glycogen may play the role of that limited resource, buffering mismatches in local energy need and energy availability via the bloodstream. Blood glucose may be practically unlimited, but utilizing glucose at a rate higher than its availability is not.

In summary, we propose that many behavioral phenomena associated with learning rates, reaction times, and mental effort avoidance can be understood as direct outcomes of constraints on information encoding and transmission. In addition to providing a parsimonious generative explanation of a range of behavioral phenomena, our approach demonstrates a successful application of the information-theoretic principles of entropy and inference to the analysis of tasks and behavior. Since Claude Shannon introduced his 'theory of communication' in 1948, there has been heated debate over whether the path between sensing and acting can be treated as a channel, in Shannon's sense, and analyzed with the tools he presented [13, 14, 15]. Shannon focused on single-channel transmissions and placed the burden of constructing efficient codes on the sender. As we show in Chapter 2, we allow information to be represented by signals across several channels, analogous to a population rate code across neurons. We also place the burden of controlling transmission duration and increasing transmission efficiency on the receiver of messages, rather than on the sender. By this shift of perspective, we provide a mechanism for producing reaction times, error rates, learning rates, and transmission costs that is consistent with information-theoretic constraints imposed on an intelligent agent acting in the environment whose statistics are only partially known. We hope our model will aid in the further application of information-theoretic concepts to the study of the information transmission in human beings.

Chapter 2

Understanding the timing of cognitive processes with a variable-length rate code

2.1 Overview

Cognitive processes all require time, as they universally depend on information transmission between brain regions limited by physical and biological constraints. The time required for behavior also exhibits surprisingly lawful variation with task demands, success and failure, stimulus and response complexity, familiarity, practice, and learning. Here we consider these regularities as consequences of constraints on information transmission, which we show provide rational predictions for timing effects across a surprising range of cognitive domains. We use a simple model for neural information transmission based on a variable-length rate code model built with Poisson processes, Bayesian inference, and an entropy-based decision threshold that simultaneously reproduces a broad array of well-known reaction-time effects. By providing a principled connection between a high-level normative decision framework with time-dependent neural rate codes, we integrate several disjoint ideas in cognitive science through translating plausible constraints into information theoretic terms.

2.2 Introduction

Whatever the task at hand, neurons performing task-related computations must infer, in a continuous-time and streaming manner, which 'messages' are being transmitted from other brain regions [16]. This inference process is noisy, imperfect, and time-dependent, and enforces a bound on behavioral reaction time to stimuli. Despite the complex and chaotic nature of neural coding, simple changes in experimental conditions have consistent and reliable effects on reaction times, described by 'laws' like the Hick-Hyman law [2, 17] and the Power Law of Practice [18]. In this chapter, we consider information transmission from the environment, through the brain, to behavior as an information channel using a neural rate code. By constraining both the channel encoding and each transmitted signal to be optimally inferred under normative assumptions, we can construct a message-transmission system that replicates these regular phenomena, and produces human-like response time distributions. Our information-theoretic approach affords a principled way to connect levels of analysis [7] by integrating energetic resource availability, message encoding and decoding schemes, and task performance characteristics into a single framework.

In what follows, we describe a continuous-time variable length coding mechanism, built using entropy and inference, that adheres to the principles of information theory while providing predictions of signal transmission time and accuracy. We emphasize that the continuous-time nature of the code means that signals are not discretized. Because of this, we are able to transmit messages such that transmission time is linearly related to message surprisal, mirroring the Hick-Hyman law. By presenting such a code, we show that many classic findings with respect to reaction time can be explained by a simple high-level neural model.

2.2.1 Background

The contributions in this chapter are conceptually derived from three concepts: signal transmission, variable-length codes, and sequential sampling. We begin the chapter with a brief introduction of each of these concepts.

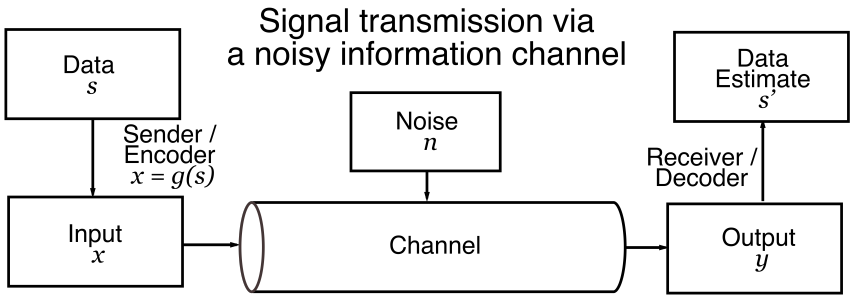

Figure 2.1: Discrete symbols are encoded, transmitted through a channel in which noise is added, and decoded to recover the original symbols. Adapted from [19], with permission, and inspired by Shannon's original diagram in [13].

Signal transmission

Signal transmission is an inferential process. In the traditional model of communication through a channel introduced by Claude Shannon [13], a sender maintains a codebook composed of a set of symbols they may wish to transmit. Symbols are encoded, either singly or in blocks, into a form appropriate for the channel (e.g. 1s and 0s for a binary channel, or into a vector of amplitudes for a Gaussian White Noise channel). During its transmission through the channel, the encoded signal may be corrupted by noise. A receiver then observes the noisy transmission and infers the nature of the message as originally encoded. This scheme is represented in Figure 2.1, redrawn from [19].

The receiver observes a noisy transmission and infers which message from the codebook was most likely to have generated the observations. In a naive scheme, it can do so by computing the relative likelihoods of the observations given each possible message, and finding the message with the highest associated likelihood. We emphasize that this decoding process happens all-at-once after a message has been received, and is not a continuous accumulation of information.

The receiver begins each transmission with an initial uncertainty, which Shannon called 'entropy' after the analogous thermodynamic concept, defined by the probability distribution P over messages X:

$$H(X) = -\sum_{x \in X} P(X = x) \log_2 P(X = x)$$

After inference, the receiver's uncertainty is reduced, but not to zero: the presence of noise in the channel introduces the possibility of transmission error. Shannon showed that the probability of transmission error can be reduced by mapping groups of messages into long 'blocks' that are not easily confusable with each other, even when corrupted by noise. Using this method, Shannon showed that entropy reduction per message, or entropy reduction per unit of time, can be maximized.

Variable-length codes

Shortly following Shannon's reconceptualization of signal transmission and uncertainty, work on data compression led to the invention of variable-length coding schemes. In a variable-length code, messages are encoded one-by-one rather than combined into blocks. Encoded message lengths are roughly proportional to the amount of information they contain. For single-symbol messages, this means that the length of each encoded messages is roughly proportional to the message's surprisal h, defined as $h(x) = -\log P(X = x)$, where $P(X = x)$ is the probability that message x will be transmitted. A message has low surprisal, and will be short, if it is sent frequently, while infrequent messages will be longer. By constructing each message's length to be related to its frequency of transmission, overall transmission time can be minimized.

Popular implementations of variable-length codes, including the Huffman code and arithmetic coding [20], are *lossless*. That is, they allow the original message to be decoded perfectly from the encoded message. This also implies a complete lack of noise in the transmission or storage process. We emphasize this, as the variable-length coding scheme introduced in this chapter allows for variable-length transmissions in the presence of noise.

Sequential sampling

In 1945, statistician Abraham Wald published a statistical procedure called the 'sequential probability ratio test' [21]. Wald was interested in making an efficient binary decision in the presence of an ordered sequence of observations $X_{1\ldots t}$. Consider the case in which observations are produced by sampling from two possible states of the world, A and B. Wald's goal was to determine, as soon as possible, which state produced the observations. His method was simple: First, specify allowable false-positive and

false-negative rates, as this determines the required degree of confidence before making a decision. Second, calculate the likelihood of observations being produced by each source, $P(X_{1...t}|A)$ and $P(X_{1...t}|B)$. Third, to test whether A is the source, compare $\log\left(\frac{P(X_{1...t}|A)}{P(X_{1...t}|B)}\right)$ to a pre-specified threshold determined by the desired error rates.

Wald's mechanism is important here for two reasons. First, Wald introduced a method for the gradual accumulation of evidence. The drift-diffusion model, commonly used to model subject response times in two-alternative forced-choice tasks [22], is a descendent of Wald's method. Second, though Wald did not have access to Shannon's concepts of entropy and decoding, he is nevertheless addressing a situation analogous to a signal transmission. In Wald's case, some property of the world constitutes the message, and observations correspond to the encoded signal. Wald's test is a decoding procedure designed to decode messages from the world with a pre-specified error rate.

2.3 Bayes-Poisson coding

In the transmission scheme described in this chapter, messages are encoded by stochastic processes and transmitted one-at-a-time in the presence of noise. The encoded message consists of a streaming sequence of observations. To decode each message, the decoder continually computes the likelihood that the noisy observations are produced by each possible source message, similar to the decoding process in Shannon's transmission system. Because the observations are streaming, the decoder does not simply select the most likely message, but tracks a likelihood distribution and updates it over time. The decoder also maintains a prior distribution over possible messages, and combines the prior with the computed likelihood to produce a posterior distribution over possible messages. The entropy of the posterior distribution reflects the decoder's uncertainty about the content of the message. This posterior entropy tends to decrease as observations are made, and the decoder makes a decision about the content of the message when the entropy reaches a pre-specified threshold.

Like Wald's procedure, this message transmission system accumulates observations over time in service of making a decision. However, rather than accumulating evidence about one of two hypotheses, the decoder accumulates *information*, in Shannon's sense of the word, allowing the decoder to decide between any number of possible messages.

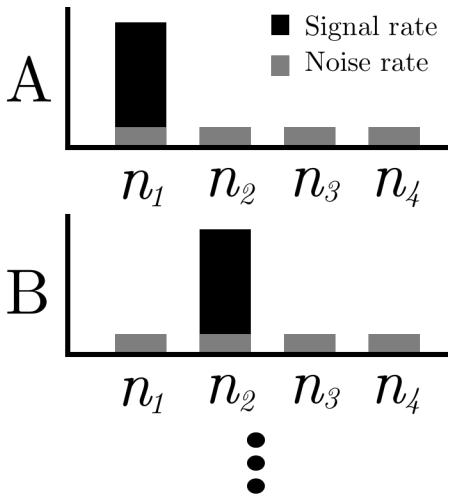

Figure 2.2: A codebook converts symbols A, B, etc. from a symbol alphabet into configurations of firing rates across Poisson processes $n_1, n_2, ...$ In this simple model, the codebook assigns a signal rate λ_S to a single Poisson process for a given symbol. Each Poisson process also emits spikes at a noise rate λ_N. As Poisson process rates are additive, this results in a total emission rate of $\lambda_N + \lambda_S$ for the 'activated' process.

The decoder's prior distribution over possible messages serves as information *a priori* about message content. As we will show, this results in variable-length transmissions, in which messages with higher surprisal, from the perspective of the decoder, take longer to transmit.

2.3.1 Implementation

We model information transmission by having a sender encode a message into a configuration of Poisson process firing rates, and having a decoder watch the generated spikes until they are confident about the configuration of underlying rates, and thus about the content of the encoded message.

The transmission mechanism consists of an encoder, a transmitter, a receiver, and a codebook. The transmitter is an array of Poisson processes, each continuously producing points or 'spikes' independently at a given noise rate λ_N. This can be viewed as a basic model of a neural rate code, as neural spike trains are often modeled as Poisson processes [16]. The symbols to be communicated are taken from an alphabet of discrete symbols $\mathcal{A}$. The codebook describes a mapping between each symbol and a configuration of

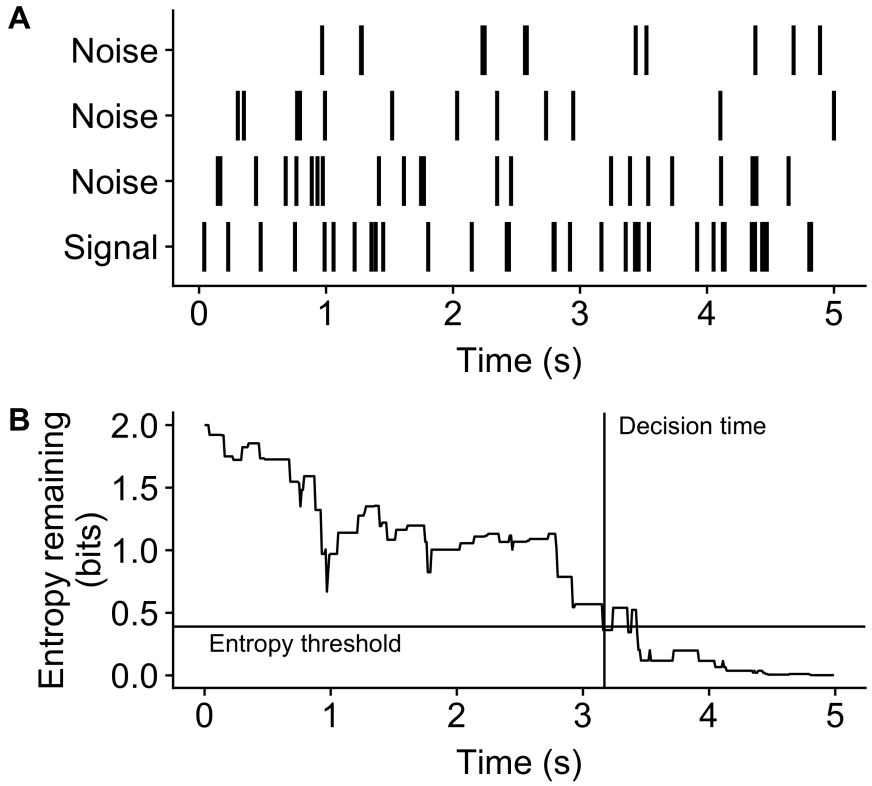

Figure 2.3: Entropy reduction for an example transmission. (A) Spikes are randomly emitted by each Poisson process as a function of time. The lower-most Poisson process is firing at a higher $\lambda_N + \lambda_S$ rate, while the others are firing at rate λ_N. (B) The decoder observes the spikes and infers which process is firing at rate $\lambda_N + \lambda_S$. The initial entropy is 2 bits, indicating an initial belief in equal probabilities for each of the 4 possible signals. The decoder's remaining entropy changes as the processes are observed and the posterior probability of each signal is calculated.

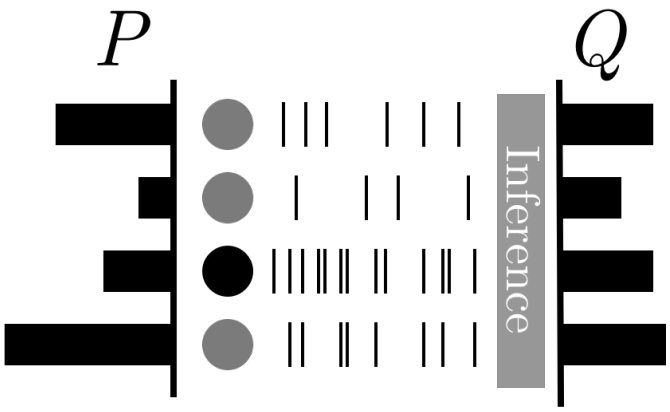

Figure 2.4: Messages are selected from a source distribution P. The codebook translates each message into a higher firing rate for a single process (a simplifying, but not restrictive, assumption). Poisson processes stochastically emit spikes, which are observed by the inference process. Bayesian inference combines the prior distribution Q with the likelihood of each message given the accumulated observations to produce a posterior distribution over possible messages.

Poisson rates. The mapping from a given symbol to rate configuration is carried out by the encoder. For the sake of expositional simplicity, we restrict the codebook to increasing the rate for a single Poisson process from the noise rate λ_N to a signal rate $\lambda_N + \lambda_S$, as shown in Figure 2.2. The neural analogue is that each Poisson process is 'tuned' to 'prefer' a particular symbol in a 1-hot manner, resulting in a sparse code.

The receiver observes the sequence of spikes emitting from each Poisson process and continuously attempts to infer which rate configuration is producing the spikes it observes, and thereby which symbol is being transmitted. We assume, again for simplicity and consistent with common information-theoretic analysis, that the receiver knows the values of both λ_N and λ_S. In standard binary or Gaussian channels, transmission is a discrete vector of amplitudes that takes a fixed time to transmit. Because of this, practitioners typically speak in terms of transmitting bits-per-signal, or bits-per-second (which are a constant multiple of each other). In our case, the receiver accumulates information about each transmission gradually, over time. In effect, observing for a longer period of time adds redundancy to the signal, decreasing the chance of decoding error.

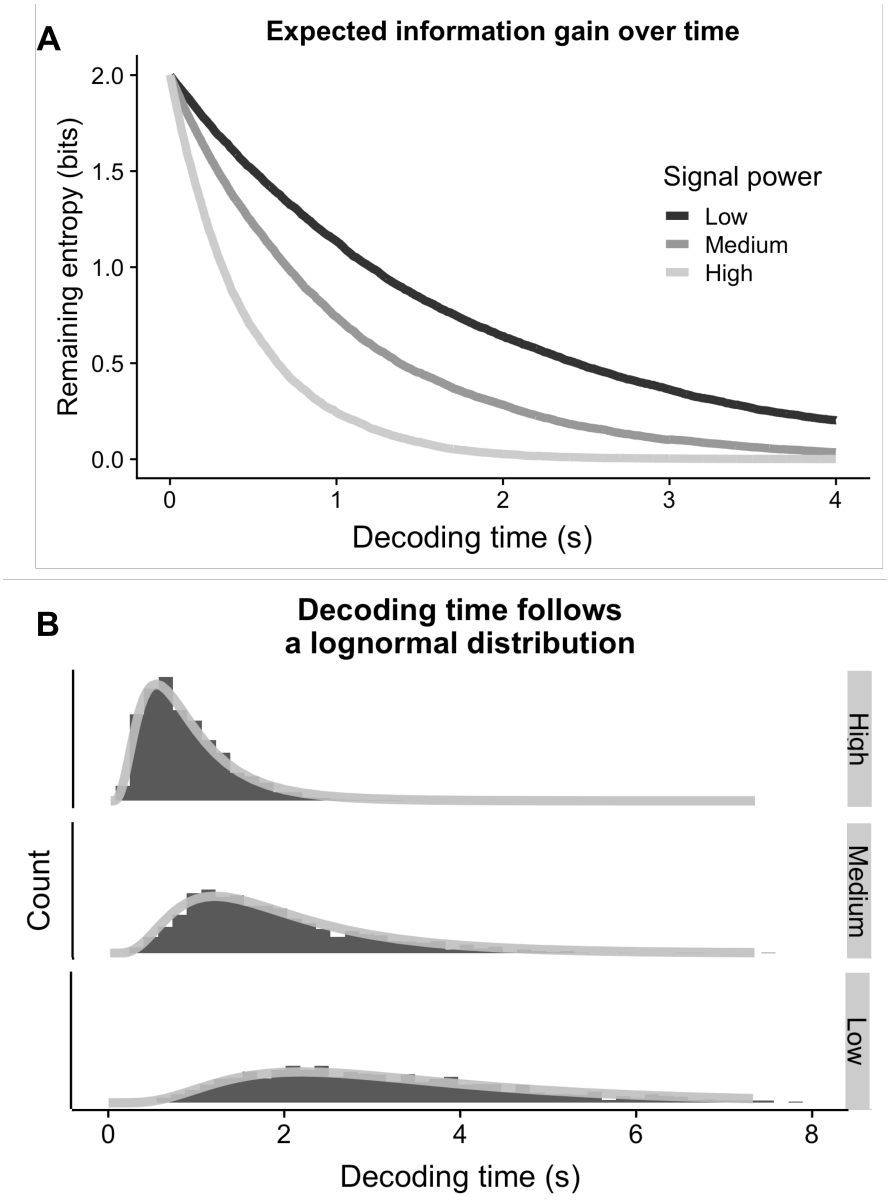

Figure 2.5: Relationship between signal power and transmission rate. (A) The expected value of the receiver's entropy regarding four possible messages decreases as spikes are observed. Increasing the signal power λ_S changes the information transmission rate. (B) Response time distributions vary as a function of signal power λ_S, and in each case are well-fit by a log-normal distribution.

As observations continue, the receiver calculates and continuously updates a posterior probability distribution over possible messages, and stops decoding when the entropy of the posterior reaches a pre-specified stopping threshold. Let transmitted symbols be treated as realizations of a random variable X. The receiver begins each transmission at time $t = 0$ with an initial uncertainty $H_Q(X)$ regarding the symbol being transmitted, reflecting its prior distribution $Q(X)$ of the possible codewords. As time passes and observations $Y_t = \{y_1, \cdots, y_t\}$ are made, the receiver uses Bayesian inference to update the prior and obtain a posterior distribution $Q_t(X|Y_t)$ over messages, which yields an updated posterior entropy $H_{Q_t}(X|Y_t)$. The posterior entropy decreases non-linearly with time and reflects the degree of confidence that a message has been correctly received, as illustrated in Figure 2.5. Transmission stops when $H_{Q_t}(X|Y_t)$ reaches a pre-set threshold. Figure 2.3 shows the change in posterior entropy over time for a single transmission.

2.3.2 Computing the posterior

Consider an example in which $p_1 \ldots p_n$ Poisson processes encode a message $m_1 \in \mathcal{A}$ by increasing the firing rate of process p_1 from λ_N to $\lambda_N + \lambda_S$, while leaving all other processes at rate λ_N. As specified above, the decoder knows the encoding scheme and the characteristics of the channel. Using this information, the decoder can calculate the posterior distribution of possible messages given observations Y_t, namely $P(m_1|Y_t)$ and each of $P(m_{i\neq 1}|Y_t)$.

Recall that the likelihood of k being drawn from a Poisson distribution with a rate parameter λ is given by:

$$p(k|\lambda) = \frac{(\lambda)^k e^{-\lambda}}{k!}$$

For a Poisson process, the likelihood distribution for observing k events in t seconds is similarly:

$$p_t(k|\lambda) = \frac{(\lambda t)^k e^{-\lambda t}}{k!}$$

To calculate the likelihood that the message encoded in observations Y_t were produced by m_1, the decoder must calculate the probability that the observations from

process p_1 were generated by a Poisson process at rate $\lambda_N + \lambda_S$ and the observations from processes $p_{2\ldots n}$ were generated at rate λ_N. To determine the posterior probability that message X is m_1 using observations Y_t, where spike counts from process i by time t are written as $Y_{it} = k_i$ we can use Bayes' rule and write:

$$\begin{aligned} P(X = m_1|Y_t) &= \frac{P(Y_t|X = m_1)P(X = m_1)}{P(Y_t)} && (2.1)\\ &= \frac{P(X = m_1)}{P(Y_t)} \prod_{i=1}^{n} P(Y_{it} = k_i|X = m_1) && (2.2)\\ &= P(Y_{1t} = k_1|X = m_1)\frac{P(X = m_1)}{P(Y_t)} \prod_{i\neq 1}^{n} P(Y_{it} = k_i|X = m_1) && (2.3)\\ &= \frac{((\lambda_S + \lambda_N)t)^{k_1} e^{-(\lambda_S+\lambda_N)t}}{k_1!} \frac{P(X = m_1)}{P(Y_t)} \prod_{i\neq 1}^{n} \frac{(\lambda_N t)^{k_i} e^{-\lambda_N t}}{k_i!} && (2.4) \end{aligned}$$

Repeating this calculation for each possible message gives a posterior distribution over all messages:

$$P(X|Y_t) = [P(X = m_1|Y_t), \ldots, P(X = m_n|Y_t)]$$

In practice, we avoid computing $P(Y_t)$ in the expressions above through normalization of $P(X|Y_t)$. The entropy of this expression, namely $H_{P_t}(X|Y_t)$, is tracked and compared to a threshold to determine when a message has been successfully decoded. In the spirit of Wald's method of evidence accumulation, the burden of delineating an individual transmission is put on the receiver of a message, rather than on the sender. This is an important departure from the typical model of information transmission.

2.4 Variable length transmissions and human reaction time

In the coding scheme introduced here, messages are *variable-length*: transmissions of messages with higher surprisal takes more time than messages with low surprisal, where surprisal is calculated using the prior probability distribution $Q(X)$ of the receiver. As mentioned above, variable-length codes produce codeword lengths (and thus transmission time of each codeword) that is roughly proportional to the surprisal of the encoded

symbol in the absence of noise. When symbols are independently drawn according to a categorical probability distribution, this can manifest in two ways. In the first, increasing the number of possible symbols increases the surprisal of each individual symbol, and consequently the length of the code needed to encode its value. In the second, symbols drawn from a categorical distribution with unequal probabilities will have different surprisal values: more frequently transmitted messages will have lower surprisal and shorter codes than less frequent messages. We performed simulations to explore these scenarios in turn using our transmission model, and discuss the results in the context of the work of Hick [2] and Hyman [17].

2.4.1 Variable codebook sizes and Hick (1952)

One of the earliest and most famous applications of Claude Shannon's "theory of communication" [13] to psychological research was a study that investigated the relationship between task demands and subject response times. In 1952, motivated by earlier observations that subject reaction times monotonically increase with the number of alternative responses in a task, William Hick performed a series of experiments in which he investigated the degree to which subject response time was related to the Shannon information of the source stimulus [2]. Hick arranged 10 pea lamps in a quasi-circular pattern, and instructed subjects (of which he was one) to gaze at the lamps, while their fingers rested on an array of "Morse keys". At regular intervals, one of the lights would be illuminated, and subjects were instructed to press the corresponding key. Lights were illuminated in "batches", and for each batch only a subset of lights were illuminated. Hick called this count the 'degree of choice' for that batch. For example, in the batch for which the degree of choice was 3, only one of three lights would ever be illuminated. In each case, lights were illuminated with equal probability, so that the information represented by each illumination is $h(x) = \log \frac{1}{P(X=x_i)} = \log n$, where n was the degree of choice for the given batch.

Hick found that, at least for the two subjects who participated in the experiment, the following relationship held:

$$RT = 0.518 \log_{10} (n + 1)$$

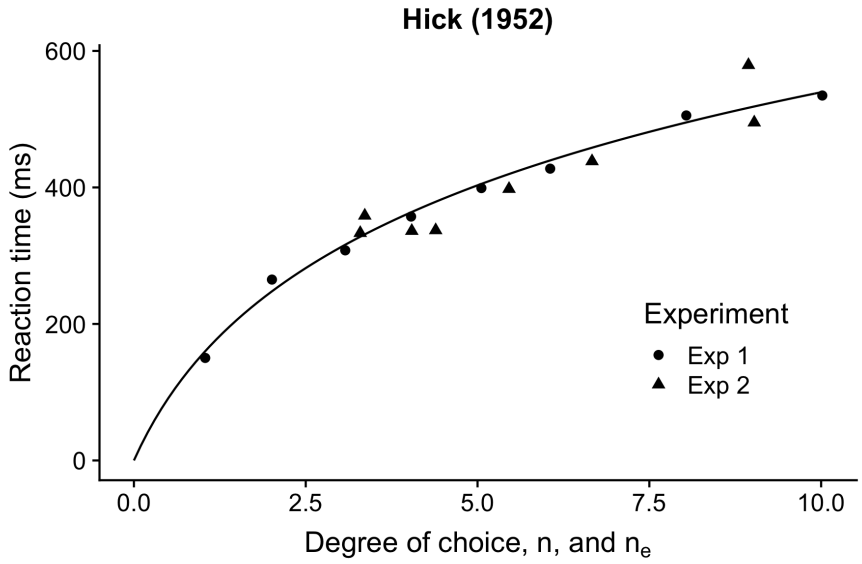

Figure 2.6: Early work by Hick [2] illustrates a logarithmic relationship between source entropy and response time, or a linear relationship between information acquisition and response time, following extensive practice. Figure replotted from [2].

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Hick concluded that response times to stimuli were determined by the amount of uncertainty (that is, entropy) in the stimulus. The +1 inside the logarithm provides a better fit for the data than merely $\log_{10} n$, and Hick justifies its inclusion by saying that subjects must know *when* a light is illuminated in addition to *which* light is illuminated, which is a source of extra information. Hick's 'provisional conclusion that information is gained at a constant rate' is known as 'Hick's law' or the 'Hick-Hyman' law. To re-phrase his conclusion, transmission time is proportional to entropy reduction.

2.4.2 Simulating the Hick-Hyman law

We simulated a scenario analogous to Hick's experiment by varying codebook sizes and recording transmission times using a pre-set entropy threshold and a uniform source distribution. The nonzero entropy threshold occasionally results in transmission errors, as we see in human subjects. Information transmitted is thus less than the surprisal of each individual message, on average. We computed actual information transmitted by calculating the mutual information between transmitted symbols and received symbols,

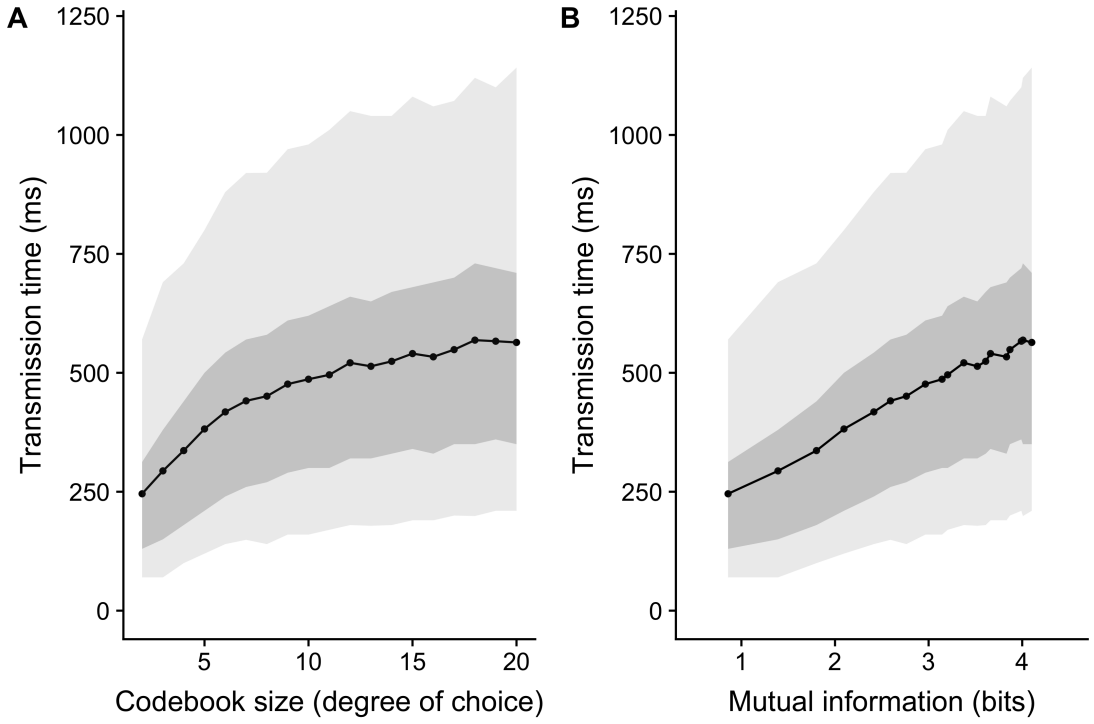

Figure 2.7: Mean transmission time increases logarithmically with codebook size and linearly with information transmitted, mirroring the Hick-Hyman law. Points represent mean transmission times and shaded regions represent the 50% and 90% high-density interval of the transmission time distribution. In each case, messages were transmitted according to a discrete uniform distribution $P(X)$ over messages, and the receiver maintained a uniform prior distribution $Q(X) = P(X)$ of the same dimensionality. For each transmission, an entropy threshold of 0.3 bits was used, with $\lambda_S = 16$ and $\lambda_N = 10$, though different rates produce different time scales. Compare with Figure 2.6.

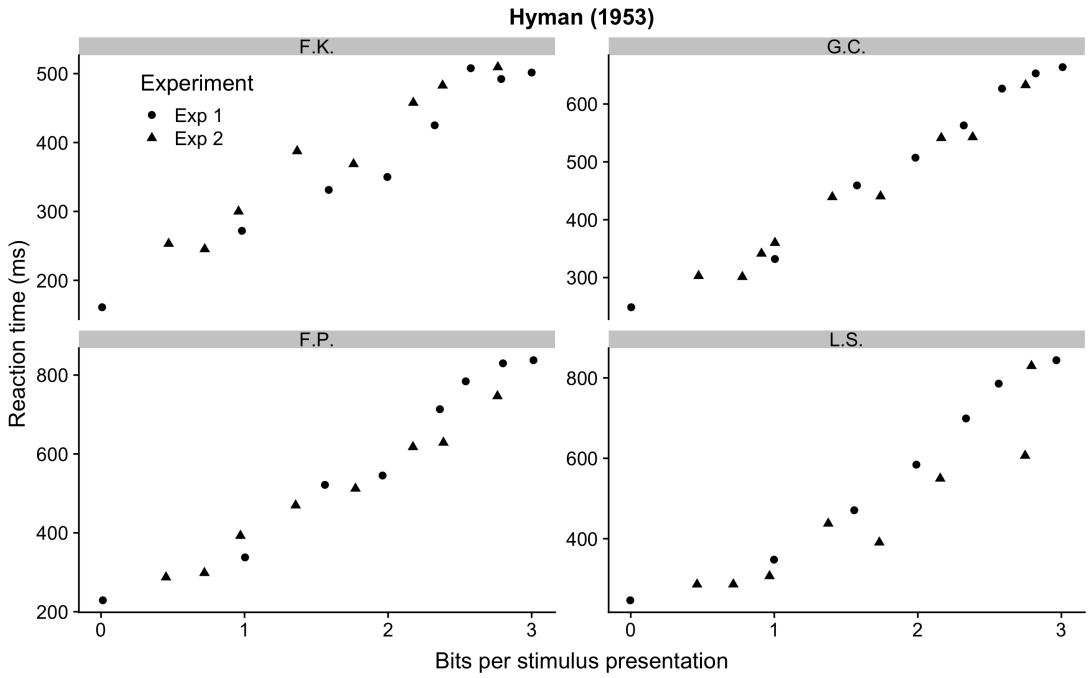

Figure 2.8: Results from Hyman (1953). Hyman found a remarkably linear relationship between stimulus entropy and response time under three different experimental conditions [17]. Hyman varied the number, relative probability, and sequential probability of stimuli in experiments 1, 2, and 3. Here, results from experiments 1 and 2 are re-plotted from [17].

for each codebook size. The results are shown in Figure 2.7 and are a close qualitative match for the Hick-Hyman observations of human response times reported in [2] and [17].

2.4.3 Non-uniform source distributions and Hyman (1953)

The next year, Ray Hyman at John's Hopkins University expanded on Hick's observations [17]. In addition to replicating Hick's finding that entropy varied with the logarithm of stimulus choices, Hyman tested two other mechanisms of entropy manipulation. First, he varied the probability distribution of stimuli, and measured the response times produced by non-uniform stimulus distributions. Second, he introduced sequential dependencies between stimulus presentations, by which any given stimulus

could be predicted, at least in part, by the preceding stimulus. Hyman showed that these other two sources of entropy manipulation produced precisely the same pattern of results, as shown in Figure 2.8.

2.4.4 Simulating Hyman's findings

We simulated a scenario similar to Hyman's second experiment from [17], in which he manipulated the source distribution of stimuli. To do this, we transmitted messages drawn from a non-uniform distribution $P(X)$ and measured transmission time for each message. For each transmission, we measured the information transmitted by comparing the receiver's prior probability distribution $Q(X)$ (which equals the source distribution $P(X)$, a critical assumption in Hyman's interpretation of his results) with its posterior distribution $Q(X|Y)$ at decision time. We measured the difference in these distributions using the Kullback–Leibler divergence between the two distributions, $D_{KL}(Q(X|Y)||Q(X))$. The change between the receiver's prior and posterior distributions is the decrease in the receiver's subjective uncertainty about which message is being transmitted. From the point of view of the receiver, this is equivalent to the amount of information transmitted, in bits. Figure 2.9 shows a linear relationship between message surprisal and transmission time, again qualitatively matching Hyman's reported results from human subjects shown in Figure 2.8.

2.4.5 Speed-accuracy trade-off

Mapping the trade-off between speed and accuracy is a common method for characterizing subject performance on tasks: subjects can favor speed over accuracy or vice versa, but their responses land on a characteristic curve describing an inherent trade-off [23]. The presence of motivational incentives can shift the shift the speed/accuracy trade-off curve in some cases [24].

We produce speed-accuracy trade-off curves by simulating transmissions with varying entropy thresholds for each of five different signal powers. The accuracy and average transmission times are plotted in Figure 2.10, and show a human-like trade-off between speed and accuracy under identical transmission conditions. Moreover, the speed-accuracy curve shifts in a predictable way in response to signal power allocation,

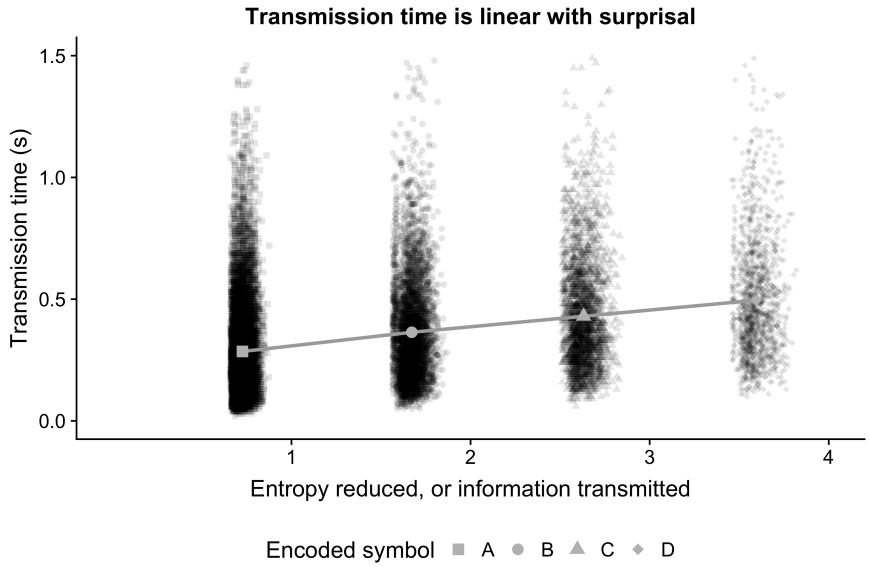

Figure 2.9: Mean transmission time increases linearly with actual information transmitted, echoing similar findings in humans by Hyman in [3]. The quantity of information transmitted is calculated as the the KL-divergence between the prior distribution $Q(X)$ and the posterior distribution $Q(X|Y)$ at decision time. Messages were drawn from a non-uniform source distribution $P(X)$. The receiver is assumed to know this source distribution and maintains a prior distribution $Q(X) = P(X)$. For each transmission, an entropy threshold of 0.3 bits was used, with $\lambda_S = 4$ and $\lambda_N = 10$. Compare with behavioral results in Figure 2.8, though note that only mean values are provided in behavioral data and variation in trial-by-trial performance is not reported.

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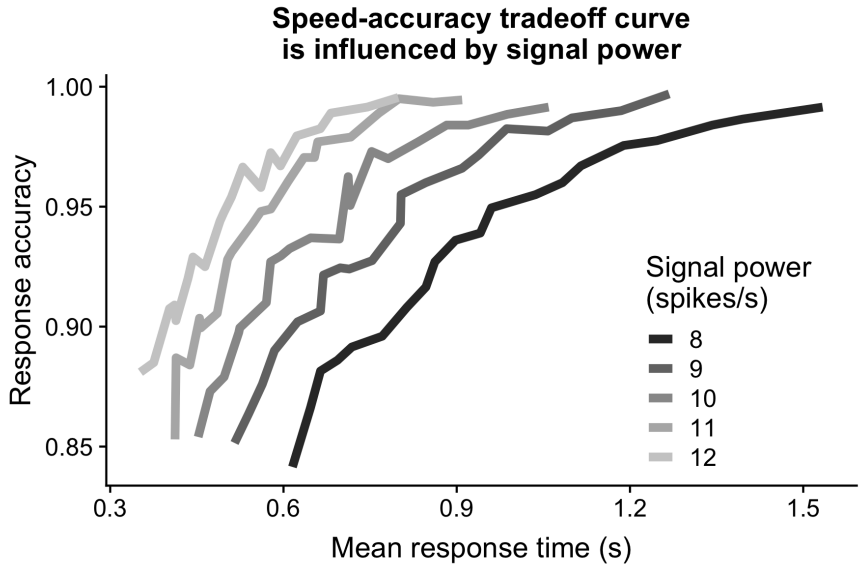


Figure 2.10: Increasing signal power λ_S shifts the speed/accuracy trade-off curve. Each curve is generated by simulating 2000 transmissions with a fixed entropy threshold. As the entropy threshold is changed, both average response time and transmission accuracy (measured as rate of correctly decoded messages) change. Simulations were performed with a noise rate λ_N of 10 spikes/s and an initial receiver entropy of 2 bits.

presenting a principled hypothesis for the mechanism of speed-accuracy curve shifts in humans.

2.5 Discussion and conclusion

In this chapter, we introduced a simple message transmission mechanism, which we call Bayes-Poisson coding, that allows information transmission in the presence of noise. Bayes-Poisson coding can be considered as a simple model of a neural rate code, but only at the computational and algorithmic levels of analysis [7]. We are not attempting to model physical neurons, but instead wish capture high-level and commonly observed properties of behavior: reliable distributions of response times, increased response times with task complexity, decreased response times with practice (see Chapter 3), and a speed-accuracy trade-off. Many of these are ubiquitous enough to have associated 'laws', which our transmission model reproduces.

Demonstrating the possibility of variable-length transmissions in a noisy environment addresses a longstanding concern with the application of information-theoretic ideas to the study of psychology. Central to this reservation appears to be a concern that Shannon's proofs of the existence of maximally efficient binary codes rely on his use of 'block codes', in which several messages are combined into a single string in a way that increases the likelihood of error-free transmission [20]. For example, Luce [15] writes that "Shannon's way of defining the concept [of channel capacity] requires that not individual signals be transmitted but rather very long strings of them so as to be rid of redundancies. That is rarely possible within psychological experiments." Another recent paper raises similar concerns that Shannon's method of encoding "requires complex computation and long delays to encode and decode in ways that achieve optimality", and that it only "applies to settings of perfect signal recovery, which may not be possible or even desirable in biological settings" [25]. It is not clear how apply Shannon's ideas of how to achieve channel capacity to psychological processes, the argument goes, so perhaps Shannon's ideas are not applicable in the study of psychology.

Concerns about the applicability of Shannon's proofs to information transmission in the brain confuse levels of analysis [7], and wrongly fixate on a supposed requirement for at-capacity information transmission. It is true that Shannon's reliance on block-coding

to achieve efficient information transmission is an implementation-level detail applicable to discrete-time codes and does not apply to the communication of information between neurons. However, the core conceptual contribution of information theory lies not in coding techniques but in providing a method for quantifying uncertainty. More broadly, it serves to characterize the ways in which noise and redundancy affect the reliability, efficiency, and rate of inference. From this broader perspective, it is surely applicable to the study of cognitive function. We have shown that by utilizing the information-theoretic principles relevant to a continuous-time system (in particular entropy and inference), and avoiding those that are not (block-coding), we can produce a simple and parsimonious explanation of a wide range of phenomena.

As with source-coding systems, expected message transmission times are faster when more frequently transmitted messages are transmitted in less time than less frequently transmitted messages. In the Bayes-Poisson model, this is implemented by tailoring the receiver's prior distribution Q to match, as closely as possible, the source distribution P. This reveals an epistemic problem from the perspective of the receiver, which has no *a priori* knowledge of the source distribution: the prior must be learned and updated by observing message transmissions.

The work of Hick and Hyman has been legitimately criticized for omitting this discussion [14]. In light of our model, Hyman's results only make sense if we assume that subjects knew, or had a good approximation of, the relative frequency of messages. Fortunately, we can assume that this is the case: Hyman had subjects practice extensively, and collected 15,000 reaction times per subject over 3 months. Though we do not have access to the data, we predict that Hyman's subjects responded to each stimulus with roughly equivalent reaction times at the beginning of training, and that differentiated reaction times arose only after practice. We discuss the relationship between task practice and transmission duration in detail in Chapter 3.

2.5.1 Relationship to the drift-diffusion model

The Bayes-Poisson model contains certain similarities to the drift-diffusion model commonly used to model two-alternative forced-choice tasks [22], but also important differences. Both models track an internal state toward a threshold, and crossing that threshold produces a correct or incorrect action. However, our model treats the source

of noise as *internal* to the decision-making process, whereas the drift-diffusion model is commonly used to model noise in the stimulus itself. In the Bayes-Poisson model, messages are models for categorical stimuli, and are static and unambiguous. Yet by including stochasticity in the transmission process itself, we produce errors and response time distributions that closely match human data. Second, our model is explicitly Bayesian. Rather than track a log likelihood ratio over two choices, tracking the entropy of a posterior distribution allows us to model tasks in which there are several possible stimuli and several choices, something the drift-diffusion model does not afford. Third, the drift-diffusion model assumes that the likelihood ratio threshold is adjusted to match a specified accuracy, which implies a certain omniscience over the long-term averaged outcomes of experimental trials by the subject. In contrast, entropy over the observed stimulus and correct response is a subjective quantity that can reasonably be tracked and updated by the subject. As we show in Chapter 4, even with a fixed entropy threshold, the model produces variations in response accuracy that depend on the prior – and these variations match human variation in task performance under the same task conditions. Finally, explicitly representing prior information as prior distributions is conceptually clearer than including a biased starting point in a drift-diffusion model.

2.5.2 Experimental predictions

The value of a model lies not only in its ability to parsimoniously explain a range of phenomena, but also in its ability to make correct predictions about new or previously unexplained data. In this chapter we have focused on a description of the model and the unified explanation it provides for a range of psychological findings related to reaction times. In Chapter 4, we model subject behavior in a novel variant of the N-back task, and show that the model makes quantitatively correct predictions about both subject accuracy and response time as a function of experimental manipulations of task structure.

2.5.3 Limitations and future work

The signal transmission model presented here, while able to reproduce an array of experimental findings, has several simplifications and possibilities for extension. The

first is that messages need not be mapped in a '1-hot' manner to Poisson process firing rates. This mapping represents one possible embedding of discrete symbols into vectors of firing rate configurations, but not the only one, and nothing in our model requires that use of a 1-hot embedding. As in traditional information theoretic analyses, good signal design requires that signals be minimally confusable and therefore 'far apart' in some representation space. When the number of messages is greater than the number of neurons, 1-hot coding is obviously impossible, and a mechanism would be needed for determining an optimal embedding of messages to rates. Conversely, it is presently unclear what an optimal coding scheme would be when the number of messages is far lower than the number of available Poisson processes. Sparse coding may still be preferable, but placing a rate cap on individual processes (analogous to a maximum signal power, a common constraint in Gaussian channels) may lead to sparse-like codes that are not 1-hot. This represents an interesting avenue for future investigation.

As presented in this chapter, we assume that the alphabet of possible messages is the same for the encoder and decoder. This constraint was imposed for simplicity, but makes it difficult to apply the model to many cognitive tasks, in which stimulus-response mappings are often many-to-few. The constraint is not necessary for the model, however, and in Chapter 4 we show how the model can be applied to understand response times and accuracy rates in the N-back task. When many stimuli are mapped to few actions, the entropy over appropriate actions, rather than over stimuli, is the quantity that must be tracked to successfully model observed behavior. This architecture affords a desirable separation of concerns between sender and receiver: the sender merely relays information about the environment, while the receiver and actor specify the confidence required to adequately perform the task at hand.

Most importantly, we currently lack a closed-form relationship between model parameters of signal power, noise power, alphabet size, entropy threshold, and message priors to the measurable outputs of response time and accuracy. Obtaining a closed form relationship, as exists for the drift-diffusion model between drift rate and response time, would afford Bayesian inference of individual subject parameters. It would also afford Bayesian model comparison of this model with other models of response time, an important technique for comparing the relative merit of competing models in accounting for experimental observations on individual tasks.

2.5.4 Conclusion

In closing, we have have introduced a principled model of information transmission, built using stochastic processes, Bayesian inference, and entropy. Our model accounts for response times as a function of both message cardinality (i.e. task complexity) and prior experience. The model incorporates the relationship between response time and response accuracy by using a simple entropy stopping threshold. Finally, we showed that the Hick-Hyman Law, log-normal response time distributions, and speed-accuracy trade-offs are all produced through placing normative bounds on the inference of source distributions and the content of individual signals. As we will discuss in Chapter 3, limited knowledge about the relative frequency of each message also places a bound on transmission efficiency, with efficiency increases mirroring the Power Law of Practice.

Chapter 3

Learning effects arise from task-indexed adaptive coding

3.1 Overview

The brain is tasked with transmitting information quickly and reliably while limiting energy use. It must encode information without perfect knowledge of stimulus statistics, making efficient encoding impossible. We consider the possibility that the brain learns task-specific codes on-line, and that the efficiency of these codes can increase with exposure to task statistics. Use of task-indexed codes would parsimoniously explain, from information theoretic first principles, a ubiquitous response time improvement during task learning called the Power Law of Learning. We also consider the implications of task-specific codes on automaticity and cognitive costs.

3.2 Introduction

Learning is characterized by adaptations of behavior which are typically assessed as increases in accuracy. During learning, however, reaction times often continue to improve after accuracy saturates [26]. Learning theories based on Bayesian statistics make predictions about changes in accuracy [27], but do not explain continued improvements in timing after accuracy saturates. We propose that improvements in response time can be explained by learning to efficiently transmit state information. We thus make

a novel proposal: learning involves both improving accuracy *and* finding efficient codes for transferring information within the brain. Using tools from information theory to instantiate this assumption, we explain how the brain could learn a code with respect to a new task; this predicts the Power Law of Learning, an power-law decay in reaction time with practice. To our knowledge, existing accounts of practice curves for response time and accuracy are either merely descriptive [18] or are part of mechanistic cognitive architectures (e.g. ACT-R [28], the instance theory of automatization [29, 30], or chunking [31, 32]).

We start with a description of a problem the brain must solve: transferring information about the state of the world from sensory areas to action selection areas, i.e. across an information channel. In order to transmit this information quickly, the brain should construct an efficient code of state information, which in turn depends on stimulus statistics and must be learned. When encountering a new task, subjects must learn many things, including which sensory information in the environment is relevant to the task (feature extraction) and which actions provide the highest reward rate over time (policy learning) as a function of time-varying circumstances (state representation). Efficiently transferring and updating state information is a problem distinct from these.

The current investigation can be seen as an application of the Efficient Coding Hypothesis (ECH) to the time scale of task learning. First proposed in the 1960s, ECH suggests that the brain develops codes designed to transmit the maximum amount of information with the fewest neural spikes [33]. This hypothesis has been supported by evidence from the visual system of the fly [34], the primate visual area V1 [35], and the retina of macaques and salamanders [36]. In each case, an efficient coding scheme is constructed using knowledge of stimulus statistics, which are learned on evolutionary or developmental time scales [37]. We propose that an analogous situation pertains to task-related information learned on-line during task engagement.

In what follows, we introduce our proposal using relevant concepts from information and control theory. We describe an ideal-observer model of the efficient transmission problem, and show that learning an efficient encoding gives rise to curves that qualitatively match practice curves seen in the literature (see Figure 3.3). We include a simple worked example with numerical simulations to demonstrate the production of response time curves as a function of coding efficiency, and show that these curves arise from

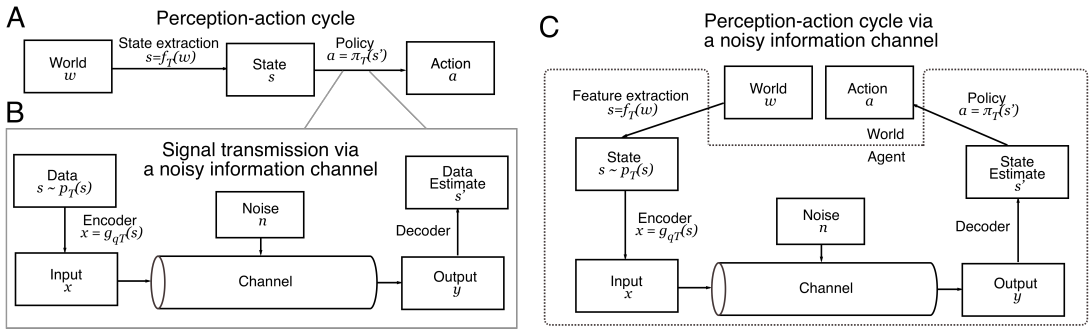


Figure 3.1: (A) Typical decision making models involve transforming observations into a state, and then using the state to select an action. (B) We claim that the transmission of state information to the action selection mechanism is subject to the constraints of information transmission: the state must be encoded and transmitted through a noisy channel. This figure is adapted from [19], with permission. (C) Taken together, we propose a refined model of action selection that accounts for transmission time, which provides a normative explanation for practice effects. State information s is encoded using a task-specific encoding (g_{QT} for a task T) using an approximation Q of the state frequency distribution P. The efficiency of this encoding depends on the quality of the estimate Q.

Binomial, Categorical, and Gaussian stimulus distributions. Finally, we show that the Power Law of Learning is produced by the Bayes-Poisson code introduced in Chapter 2. We discuss the relationship between the current work and adaptive codes in the visual system, as well as implications for understanding automaticity and cognitive costs.

3.3 Efficient state encoding

When behaving on-line in an ecological environment, an organism must represent environmental information sufficient to afford action selection. We assume that this information must be transmitted from the senses, through the brain, which will eventually result in an action. In this context, the brain acts as an information channel, transmitting information between sensory input and action output.

While our approach is reminiscent of applications of information theory to psychology from the 1950s and later (see [5] for a review), we explicitly restrict ourselves to David Marr's computational level of analysis [7], in which we investigate the problem the

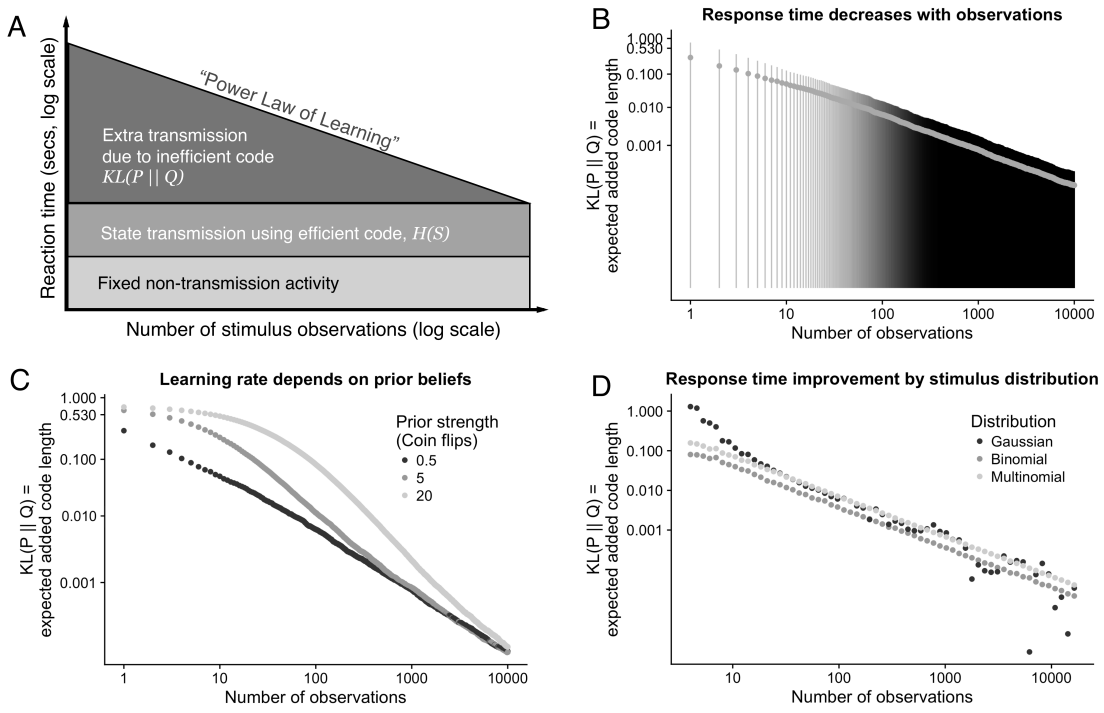


Figure 3.2: (A) Response time is composed of fixed time costs (including the cost of efficiently transmitting state information), plus extra transmission time due to use of an inefficient code, which decreases with practice. (B) This figure shows change in $KL(P||Q)$ as flips of a biased coin are observed, averaged across many subjects. $KL(P||Q)$ measures the inefficiency of state encoding, and decreases linearly in log-log space. This mirrors the Power Law of Learning, an example of which is shown in Figure 3.3. Grey lines represent 1 SE of non-transformed values. (C) A strong, incorrect prior on the state frequency distribution initially slows learning. Each line represents a different strength prior belief that a biased coin is actually unbiased. (D) The power-law relationship holds for observations of state spaces following Binomial, Categorical, and Gaussian distributions. In each simulation, values are averaged across 2000 simulated subjects.

brain is trying to solve: transmitting stimulus information quickly over a finite-capacity channel.

Problem description

We borrow from control theory and say that information about the world is compressed into a state s, where the space of possible states S and the world-information-to-state mapping are determined by the task being performed. Once the value of the state s is computed (say, for a single trial of an experiment), it must be transmitted to an action selection mechanism. In order to be transmitted over a channel, s must be encoded into a form transmissible by the channel medium (in this case, the brain). In accordance with the computational level of analysis, we need make no claim about the form of the code, except to point out that that the same information can be transmitted using either efficient or inefficient codes. Nevertheless, at the end of the current chapter we discuss how the application of efficient coding principles to the Bayes-Poisson code introduced in Chapter 2.

We treat the state as drawn from a probability distribution $P(S)$. In general, the quantity of information that must be transmitted in order to specify the state is equivalent to the entropy of the state space:

$$H(S) = -\sum_{s \in S} P(S = s) \log_2 P(S = s)$$

In an efficient variable-length code, the average code length assigned to each value of s is proportional to $-\log_2 P(S = s)$. As such, constructing an efficient code requires knowledge of the distribution of $P(S)$ [20].

Inefficient code length

Critically, $P(S)$ must be learned from experience, as individuals engaged in a new task do not know the state frequency distribution. An inefficient coding of a state s will result in a longer transmission than an efficient code. Assume that an inefficient code is constructed using an estimate of the state space distribution $Q(S)$. The extra code length is defined by the Kullback-Leibler divergence between the two distributions, usually written as D_{KL} or KL:

$$KL(P||Q) = \sum_{s \in S} P(S = s) \log_2 \frac{P(S = s)}{Q(S = s)}$$

As an individual performing a task observes more realizations of the stimulus state, they can update Q, and with many observations $KL(P||Q) \to 0$. This in turn allows the subject to construct an (approximately) efficient code, transmit state information in a minimum amount of time, and select an action more quickly. Thus, reaction times directly depend on the efficiency of state encoding.

A simple example

Suppose an individual is engaged in a task in which they observe the outcome of a coin flip. They are instructed to press a left arrow key if they observe heads, and a right arrow key if they observe tails. The image of a coin must be processed visually and turned into a state $s \in S$ (object recognition or feature extraction), and the mapping between flip outcome and response is learned (policy learning). These processes contribute to response accuracy. In addition, the state of each flip must be encoded and transmitted through the brain to an action selection mechanism that in turn drives a key press. This second process contributes to response time.

Suppose the probability of a biased coin landing on heads was $P(S = \text{heads}) = 0.9$, and each flip is modeled as being drawn from a Bernoulli distribution. For an unbiased coin, the stimulus encoder mechanism (sender) could transmit $\log_2 2 = 1$ bit of information to the action selector mechanism (receiver). If the sender knew the bias of this particular coin, it would only need to transmit $H(S) = -(0.9 \log_2 0.9 + 0.1 \log_2 0.1) = 0.47$ bits, on average, to specify the outcome of each coin flip.

Assume that the sender has a prior belief that the coin is unbiased, and thus has an estimate Q_{init} of P. This subjective ignorance means that the sender is unable to construct an optimal code. Hence, the sender would construct a code that requires 0.53

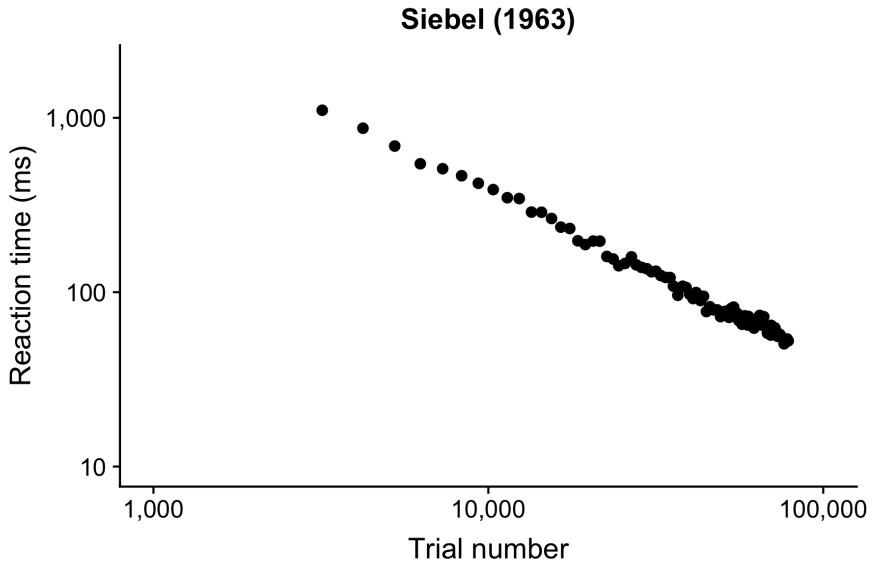


Figure 3.3: The Power Law of Learning, also called the Power Law of Practice, describes a power-law relationship between practice trials and response times. Given the inherent noise in behavioral data and variable learning rates of individuals, the Power Law is only apparent after averaging across subjects. However, the trend holds for a surprisingly wide range of tasks, including reading inverted text, scanning for visual targets, performing geometry proof justification, mirror tracing, and more. See [18] for a review. Figure was replotted from [18], which reported data from [38].

extra bits, on average, to communicate the outcome of a coin flip:

$$\begin{aligned} KL(P||Q_{init}) =& \sum_{s \in S} P(S=s) \log_2 \frac{P(S=s)}{Q(S=s)} \\ =& 0.9 \log_2 \frac{0.9}{0.5} + 0.1 \log_2 \frac{0.1}{0.5} \\ =& 0.53 \end{aligned}$$

3.3.1 Power Law of Learning

As the sender observes more coin flips, its estimate Q_{init} of P improves to Q_{obs}, and the sender's code becomes more efficient. To investigate the characteristics of this update, we simulated 10,000 coin flips for each of 2,000 subjects. For each flip we calculated the maximum likelihood estimate Q_{obs} of P using every observed flip to that

point, effectively incorporating observations into the count parameters of a Dirichlet distribution. We then calculated $KL(P||Q_{obs})$, and averaged the KL-divergence across all subjects for each number of flips. Results are shown in Figure 3.2. When subjects have a weak prior, the code length improvement has a linear relationship with stimulus observations when plotted in log-log space, exactly like the Power Law of Learning [18]. However, the initial rate of average code length decrease depends on the strength of subjects' prior beliefs that the coin is unbiased. Code length improvement rates as a function of prior strengths are shown in Figure 3.2C.

In our simulations, the power-law relationship is clearest when our virtual subjects have weak priors on stimulus statistics. Accordingly, we suspect that the Power Law of Learning arises as an experimental result exactly because this is akin to the scenario in many psychology experiments, in which subjects are unfamiliar with the task and have a weak prior on stimulus statistics. The existence of strong, incorrect prior beliefs results in qualitatively different learning curves, an experimentally testable prediction.

Generalizability

In the coin flip example, we focus on encoding the value of draws from a Bernoulli distribution and show power-law decreases in transmission time. In Figure 3.2D, we show similar results for both Categorical ($k = 16$) and univariate Gaussian distributions. These simulation results suggest that the trend may not depend on the specific parameters or form of the state distribution. Interestingly, each case results in a power-law exponent of -1. Power law fits to response time curves in the experimental literature give exponents between 0 and -1 [18], indicating a slower rate of learning in real subjects than the ideal observer model presented here. See Section 3.3.2 below for related discussion.

Aggregating across subjects

In the psychology literature, the smooth linear curves described by the Power Law of Learning arise as a result of averaging across many subjects. This observation has been leveled against Power Law of Learning as a criticism [39], but as we show below, this power-law decay is an effect of aggregating many subject response times when each subject is learning optimally. Indeed, an organism using efficient coding should

have trial-to-trial response time variance related to both their updated code and the information content ('surprise') of each observed state. In other words, each subjects' trend during learning is not expected to be smooth. The between-subject variance of simulated response times is shown as vertical gray lines in Figure 3.2B.

3.3.2 Learning rates

In each of the simulations presented above, the slope of the Power Law line is -1, indicating a power-law decay exponent of -1. As mentioned above, exponents recorded in the literature are exclusively between 0 (no learning) and -1 (presumably, a maximum learning rate). Table 3.1 from [18] shows several experimentally determined learning rates.

The exponent of the power-law, and consequently the learning rate and slope of the log-log plot, varies if we implement an *anchoring bias* [40] in the distribution update step. In doing so, we are suggesting that distribution updates are conservative. As noted above, we estimate the distribution Q by observing categorical counts, and updating the count parameters in a Beta or Dirichlet prior distribution over proportions. In a fully Bayesian update, each observation causes the corresponding parameter to increment by 1, giving a new maximum likelihood estimate of the relevant proportions.

In order to implement an anchoring bias, we perform a recursive *anchored* update of outcome proportions after each observation. To follow the coin-flip example, suppose we have a Bernoulli proportion p, and a set of N observations, of which H are heads. At each time step t, the update step is as follows. Let our new observation $Y = 1$ if the observation at time step t is heads, and $Y = 0$ otherwise. For a fully Bayesian update, a recursive update form would be:

$$p_{t+1} = \frac{p_t N + Y}{N + 1}$$

In this formulation, the numerator represents the past count of 'heads' observations, plus the value of the new observation Y. The denominator represents the count of total observations, plus one new observation. An anchored update in the same form is as follows:

Data Set	B	α
Snoddy (1926)	79.20	.26
Crossman (1959)	170.1	.21
Kolers (1975) - Subject HA	14.85	.44
Neisser et al. (1963)		
Ten targets	1.61	.81
One target	.68	.51
Card, English & Burr (1978)		
Stepping keys - Subj. 14	4.95	.08
Mouse - Subj. 4	3.02	.13
Seibel (1963) - Subject JK	12.33	.32
Anderson (Note 1) - Fan 1	2.358	.19
Moran (1980)		
Total time	30.27	.08
Method time	19.59	.06
Neves & Anderson (1980)		
Total time - Subject D	991.2	.51
The Game of Stair		
Won Games	1763	.21
Lost games	980	.18
Hirsch (1952)	10.01	.32

Table 3.1: Experimentally measured power-law slopes. Reproduced in part from [18]. Parameters correspond to the power-law equation $T = BN^{-\alpha}$, where N represents practice trials, T is response time, and B and α are constants. All power law slopes, indicated by α in the table, are between 0 and -1.

$$p_{t+1} = (1 - \alpha)p_t + \alpha \cdot \left(\frac{p_t N + Y}{N + 1}\right)$$

Here, we start with the old term, and add a weighted difference between the full updated value and the old value. When the weighting term $\alpha = 0$, we have $p_{t+1} = p_t$ for each iteration, and no learning occurs. When $\alpha = 1$, we obtain the full update:

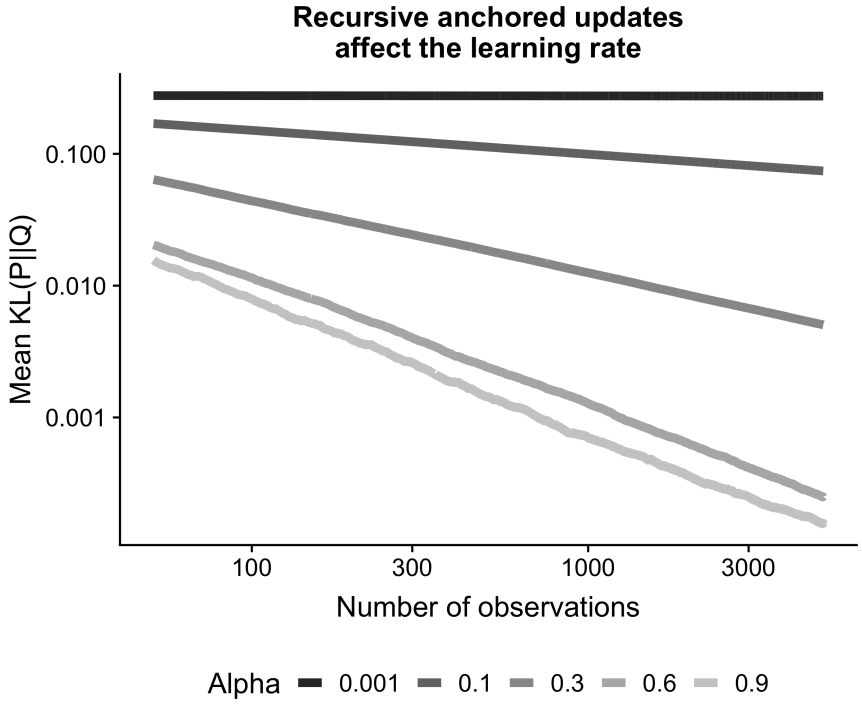


Figure 3.4: Varying the level of anchoring controls the learning rate, as reflected in the slope of the log-log plot.

$$
\begin{aligned}
p_{t+1} &= (1-\alpha)p_t + \alpha \cdot \left(\frac{p_t N + Y}{N+1}\right) && (3.1)\\
&= 0 \cdot p_t + 1 \cdot \frac{p_t N + Y}{N+1} && (3.2)\\
&= \frac{p_t N + Y}{N+1} && (3.3)
\end{aligned}
$$

Figure 3.4 shows power-law slopes for varying values of α. Leider et al. [41] suggest that such anchored adjustments may represent an optimal strategy when updates are costly. If so, α would be inversely related to the update cost.

Updating the proportion p_t of 'heads' and 'tails' can be equivalently written as a partial update to both heads and tails counts. Let H_t and T_t be the count of heads and tails, respectively, at time t. Letting $Y = 1$, indicating a flip of heads, we can re-write

the update above as:

$$p_{t+1} = (1-\alpha)p_t + \alpha \cdot \left(\frac{p_t N_t + 1}{N_t + 1}\right) \tag{3.4}$$

$$\frac{H_{t+1}}{N_t+1} = (1-\alpha)\frac{H_t}{N_t} + \alpha\frac{\frac{H_t}{N_t}N_t + 1}{N_t+1} \tag{3.5}$$

$$\tag{3.6}$$

Multiplying by $N_t + 1$ gives:

$$H_{t+1} = (1-\alpha)\frac{H_t(N_t+1)}{N_t} + \alpha\frac{H_t+1}{N_t+1}(N_t+1) \tag{3.7}$$

$$= \frac{H_t(1-\alpha)(N_t+1)}{N_t} + \alpha(H_t+1) \tag{3.8}$$

$$= \frac{H_t(N_t+1-\alpha N_t-\alpha)}{N_t} + \alpha\frac{H_tN_t+N_t}{N_t} \tag{3.9}$$

$$= \frac{H_tN_t+H_t-\alpha N_tH_t-\alpha H_t)}{N_t} + \frac{\alpha H_tN_t+\alpha N_t}{N_t} \tag{3.10}$$

$$= \frac{H_tN_t+H_t-\alpha H_t+\alpha N_t}{N_t} \tag{3.11}$$

$$= H_t + \alpha + (1-\alpha)\frac{H_t}{N_t} \tag{3.12}$$

When $\alpha = 1$, the new count becomes $H_{t+1} = H_t + 1$, as described above. Critically, we enforce the total added count across all outcomes to sum to 1. Not enforcing the incremental count updates to add to 1 destroys the power-law relationship. The corresponding update for the count of tails:

$$T_{t+1} = T_t + \left(1 - (\alpha + (1-\alpha)\frac{H_t}{N_t})\right) \tag{3.13}$$

Notice that when $\alpha = 0$, $H_{t+1} = H_t + \frac{H_t}{N_t}$. As this update has a corresponding update for tails of $T_{t+1} = T_t + (1 - \frac{H_t}{N_t})$, the relative proportion of heads does not change:

$$\frac{H_{t+1}}{N_t+1} = \frac{H_{t+1}}{H_{t+1}+T_{t+1}} \tag{3.14}$$

$$= \frac{H_t + \frac{H_t}{N_t}}{H_t + \frac{H_t}{N_t} + T_t + (1 - \frac{H_t}{N_t})} \tag{3.15}$$

$$= \frac{N_t H_t + H_t}{N_t} \cdot \frac{1}{H_t + T_t + 1} \tag{3.16}$$

$$= \frac{H_t(N_t+1)}{N_t(H_t+T_t+1)} \tag{3.17}$$

$$= \frac{H_t(N_t+1)}{N_t(N_t+1)} \tag{3.18}$$

$$= \frac{H_t}{N_t} \tag{3.19}$$

$$\tag{3.20}$$

A similar computation can be performed for the proportion of tails. Performing count updates by distributing evidence from an observation across multiple counts can be thought of as a *noisy update*, where the fact of an observation is recorded but its allocation to count parameters is determined by some learning rate – in which case, the learning rate might be better thought of as a *evidence attribution* effectiveness. It is interesting that anchored updating, which is typically interpreted as a bias resulting from costly updates, can be re-written in terms of evidence attribution.

3.3.3 The Power Law of Learning in the Bayes-Poisson code

In Chapter 2, we demonstrated that the time taken to transmit a signal using the Bayes-Poisson code was related to the degree of change in belief by the receiver of a message about the message content. Receiver prior belief is captured by a distribution $Q(X)$ over possible messages, which is updated to a posterior observation $Q(X|Y)$ after observations Y are made. Suppose we allow a receiver with an incorrect uniform prior message distribution Q_{init} to update its distribution to Q_{obs} in a Bayesian manner each time a message is received, so that the subsequent message transmission starts with the updated prior. Since the receiver begins with a uniform prior, each message should take roughly the same amount of time to transmit, regardless of the actual source distribution

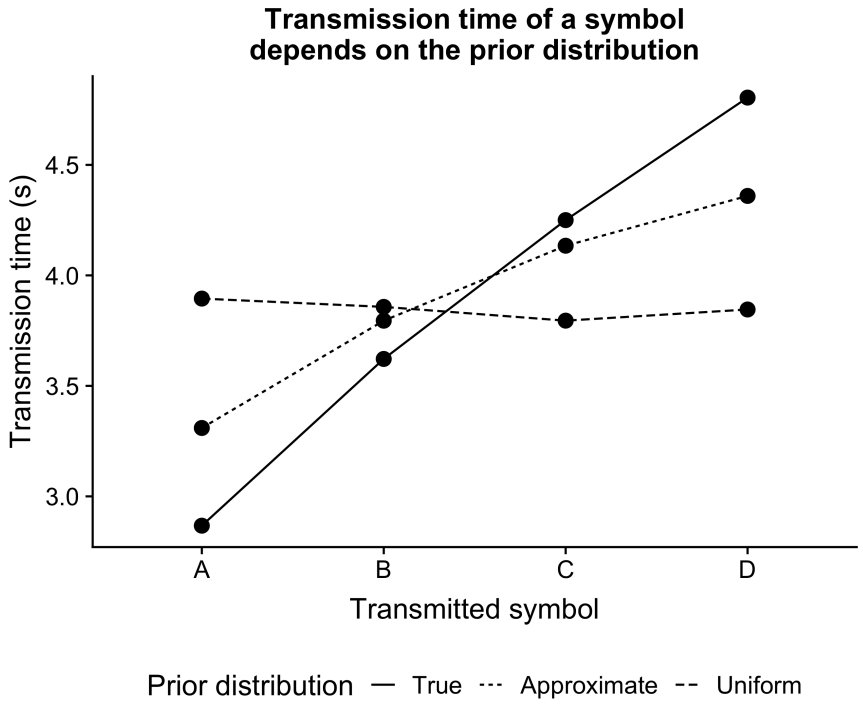


Figure 3.5: Strong prior beliefs slow learning. Mean transmission time is a function of the receiver's prior belief $Q(X)$ over messages, rather than the source distribution $P(X)$. In each case, messages were transmitted from the identical source distribution, where A was most frequent, followed by B, and so on. Each line connects response times arising from the same prior distribution $Q(X)$. A uniform $Q(X)$ results in a flat line, while a $Q(X) = P(X)$ results in the steepest slope. In each case, the relationship between subjective surprisal and response time is approximately linear. For each transmission, an entropy threshold of 0.3 bits was used, with $\lambda_S = 4$ and $\lambda_N = 10$.

of messages. As the receiver observes which messages are transmitted and at what relative frequency, Q_{obs} will become an ever-closer approximation to P, shrinking both $D_{KL}(P||Q_{obs})$ and the expected transmission times.

Figure 3.5 illustrates a change in transmission times for four messages A, B, C, and D, in which A is more frequent than B, and so on. As more messages are transmitted and the initial uniform Q approaches the true distribution P, transmission time for frequent messages decreases, while transmission time for infrequent messages increases.

To characterize the rate at which updates to Q influence message transmission times,

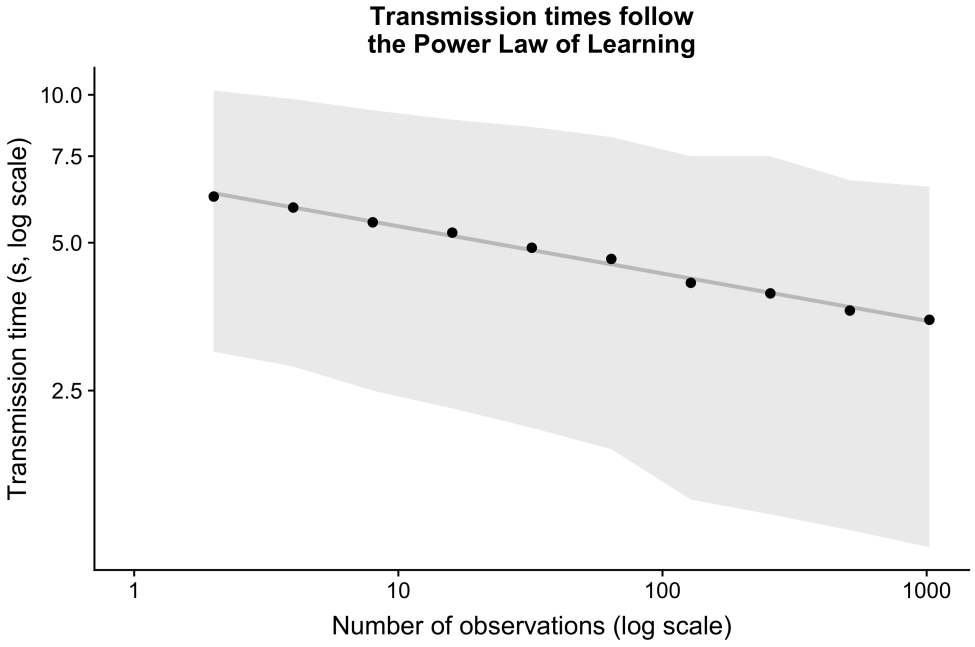


Figure 3.6: Simulated message transmission time decreases as a function of observations, as the prior Q approaches the source distribution P. Signals are transmitted using the Bayes-Poisson code described in Chapter 2, with signal strength $\lambda_S = 4$, noise power $\lambda_N = 10$, and an entropy threshold of 0.3. Points represent mean transmission times, and the shaded region represents the 80% high-density interval of the response time distributions. Compare with the behavioral results in Figure 3.3.

we constructed a categorical source distribution P with $k = 16$ categories, but with most of the probability mass in two categories:

$$\begin{aligned} P = \quad & [0.005, 0.005, 0.005, 0.005, 0.005, 0.005, 0.005, 0.005, \\ & 0.005, 0.005, 0.005, 0.005, 0.005, 0.005, 0.465, 0.465] \end{aligned}$$

We initialized Q_{init} to have a Dirichlet prior with concentration parameters 2, representing a weak prior belief that the source distribution is uniform. We simulated N message transmissions, for $N = 2$ to $N = 1024$, taken evenly in log space. For each value of N, we averaged the results across 1,000 simulated observers, resulting in an expected posterior distribution Q_{obs} after N observations. For each Q_{obs} we then simulated more 2,000 message transmissions, with messages drawn with frequency defined by P, and calculated the transmission time for each. As illustrated in Figure 3.6, the relationship between observations N and transmission time is linear in log-log space, matching the Power Law of Learning.

3.4 Discussion and conclusion

In this chapter, we introduced a normative theory of task-specific efficient code learning. This theory provides a generative explanation for the Power Law of Learning without specifying a particular decision model. Our only requirement on the decision process is that the state information for a task be transmitted through a finite-capacity channel. As such, this theory can be integrated into other decision making frameworks, in particular neural or dual-processing theories.

Neural plausibility

The Efficient Coding Hypothesis describes a principle for optimal information transmission over the lifespan of an organism interacting with their environment; adaptation occurs on the evolutionary or developmental timescale. Recent evidence suggests that neural codes can also adapt at the millisecond timescale, apparently in order to maintain a high degree of information transmission in the face of rapidly changing stimulus

statistics [42, 43]. These findings suggest that the Efficient Coding Hypothesis may also apply to a fast temporal scale in addition to the relatively static tuning curves and cell sensitivities that are the typical focus of analysis. In our view, such findings support the plausibility of task-specific code adaptation.

Relation to automaticity

Work on automaticity and implicit learning emphasizes that attentional capacity, response time, accuracy, and multitasking performance all increase with practice and the development of expertise in a task [29]. However, these improvements appear to be strongly tied to specific tasks and environments. Learning task-specific coding suggests a normative account of these effects. When transmitting information over a limited-capacity channel, on-line learning of an efficient code enables more information to be transmitted in a given time. We suggest that task automaticity may be equivalent to learning an efficient task-specific code. We call task-specific code building *adaptive* because it involves adapting a neural code to a specific task.

Cognitive costs

Cognitive operations are referred to as 'costly' when they give rise to subjective fatigue and behavioral aversion (see [44] for a recent review, and Chapter 5 for further discussion). We note that task aversion often subsides with practice and the development of task-specific expertise, which appears related to the development of task automaticity. For that reason, we speculate that decrease in cognitive costs with practice may be a direct result of learning an efficient encoding of task states, and conversely that the costs themselves arise from transmitting information using inefficient codes. Minimizing transmission costs may also reduce metabolic costs, which we propose to be a primary driver of cognitive costs. See Chapter 6 for further discussion.

Limitations and future work

We have proposed that the brain learns efficient codes on-line, but have intentionally avoided specifying neural implementation details. In order to model behavioral data

from a specific task, we would need to specify a full decision model, an encoding algorithm, and the characteristics of the information channel, e.g. channel noise. Our current analysis serves as a normative ideal-observer model against which actual behavioral data can be compared.

Chapter 4

Information integration from multiple sources in the N-back task

4.1 Overview

The N-back task is considered to be a prototypical working memory task, but performance on the task correlates poorly with other tasks that measure working memory capacity [45, 46]. Recent work suggests that subjects may exploit N-back task structure to improve performance, raising the question of whether responses solely reflect working memory or also include the leveraging of additional information [47]. To test this we modified the traditional N-back task to introduce sequential structure in target responses, which predicted responses either conflicting with or congruent to the target response, similar to the Stroop task. Subjects exhibited higher accuracy and faster responses on congruent trials than incongruent trials. To account for change in performance, we simulate behavioral data using a model in which task statistics, past responses, and past images combine to inform prior distributions on current stimulus and response probabilities. We suggest that performance on the N-back task has been largely misinterpreted, and that subjects exploit a wider array of information sources than is normally assumed.

4.2 Introduction

The N-back task [48, 49] is often thought of as a prototypical working memory task and is one of the most commonly used experimental paradigms in cognitive psychology research. In the task, subjects are shown a series of stimuli and asked to state whether each stimulus is the same as, or different from, the stimulus observed N trials previously. The N-back task has become the 'gold standard' used to investigate the neural correlates of working memory [50, 51], in part because it is thought to involve encoding, maintaining, and deleting items in memory, and in part because the task design only requires simple responses [46, 52]. In addition, the N-back task also affords the manipulation of working memory load with N.

Despite its widespread use as a working memory task, the construct validity of the N-back task has been called into question [45]. Performance on the N-back correlates weakly with simple working memory span [45] and reading span [53] (though see also [54]). It correlates not at all with the digit span backward task [55, 56]. Performance seems to correlate more strongly with recognition tasks and more complex tasks like the Sternberg task [53], the operation span task [54], and the Stroop task [57], though results vary with the exact version of the task used. Performance on the N-back task seems to correlate weakly with simple tasks in general, though some studies have used composite scores to achieve greater correlation with N-back performance [46].

Analysis of published research reveals significant heterogeneity in stimulus design choices and corresponding variation in both task performance itself and performance correlation with other tasks [47, 46]. Such variation in performance across experiments despite *prima facie* similarity of the task requirements suggests that subject responses may be influenced by the structure of the task itself in addition to information about previously observed stimuli explicitly represented in working memory. For example, a robust source of error in the N-back task is the presence of 'lures', in which the stimulus shown $N-1$ or $N+1$ previously matches the current stimulus, but the stimulus shown N previously does not [45]. Errors on lure trials are consistently higher than on control trials, presumably because lures elicit a familiarity-based response, but researchers rarely report the presence or frequency of lure trials in task descriptions [47]. Other variation in task design includes the size of the set from which images are drawn and

the relative frequency of 'target' ('same') responses, whether the stimulus is presented aurally, symbolically, or spatially, and finally whether the stimuli are presented as a long stream or a sequence of short sets.

If lure frequency, relative response frequency, or vocabulary sizes influence performance on the N-back task, then resulting variations in performance could be understood as involving the combining and weighting of information to generate a response that reflects multiple sources of input. In addition to information from stimulus familiarity and working memory representations, a task structured to have mostly responses of 'different' might lead a subject to bias responses towards 'different' irrespective of the value of the currently observed stimulus. When viewed from this perspective, the N-back might be better understood as an executive function task with a working memory component, rather than a working memory task *per se* (see [47, 45] for further discussion).

Combining information to create a response also highlights an unexpected similarity between the N-back task and cognitive control tasks. Any structure-driven response may either be congruent to, or conflict with, a recall-based response, dividing trials into *congruent* and *incongruent* trials [47]. This is similar in structure to the Stroop and Flanker tasks [9, 8], in which the task is explicitly (rather than accidentally) designed to produce compatible or conflicting response impulses. In those tasks, conflicting responses are characterized by higher error rates and longer response times than congruent responses. A typical interpretation is that conflicting responses require cognitive control to overcome the response encouraged by the information stream incompatible with the task instructions [58, 59, 60].

While the effect of lures on familiarity-driven N-back responses is well-characterized, less is known how higher-level task statistics affect N-back responses. In this chapter, we report the results of an experiment in which we sought to explicitly test the analogy of the N-back task as a cognitive control task, and determine whether it is possible to influence subject behavior by manipulating the statistical structure of the task. We designed a set of N-back stimuli with a sequential regularity in the target responses of certain blocks. Subjects were not explicitly made aware of the structure. The sequential regularity took the form of of the sequence $SDSDSD...$, where S indicates that image shown N previously was the same as the currently visible image, and D indicates that it is different. In such 'patterned' blocks, individual trials are divided into congruent

responses, in which the response pattern predicted the same response as the N-back instructions, and incongruent responses, in which they predicted opposite responses. In 'random' blocks, responses are still balanced, but the sequence is randomly ordered.

We modeled subject responses as being generated using the variable-length code presented in Chapter 2. In this model, statistical information from task structure and past stimuli is encoded into prior distributions utilized by signal observers to decode the current image, and to determine actions based on the current and past images. In the Bayesian formulation, a prior distribution is information present *a priori*, that is, prior to an observation. When the prior is congruent with a current observation or response, less information needs to be transmitted to achieve a given entropy threshold, and this shortens response time. On the other hand, when a prior is incongruent with a given observation or response, the information encoded in the prior must be overcome by information observed on the current trial. This takes more time, causing response times to lengthen. In essence, response time effects of congruent and incongruent stimuli are predicted because (a) transmitting information takes time, and (b) information driving an action comes from both the current stimulus and the prior, which is informed by both past stimuli and the statistical structure of the task. The presence of a strong prior also biases responses, creating a predictable pattern of decoding and response errors.

We compared N-back performance on congruent and incongruent trials with performance on random blocks, in which there was no pattern in the target responses. As expected, our task elicited a pattern of behavior compatible with traditional cognitive control tasks: subjects responded more quickly and accurately on congruent trials than neutral trials, and more slowly and with a higher error rate on incongruent trials. In addition, we report response time differences for 'same' vs 'different' responses, which are also predicted by our model.

That subject behavior is consistently influenced by the presence of statistical structure in the N-back task is strong evidence that the N-back task is not solely a working memory task, and that it contains structural similarities to cognitive control tasks. Moreover, model results exhibit a close qualitative match with subject responses, correctly predicting the way in which responses are manipulated in the presence of statistical structure. The model matches human behavior with respect to changes in response

accuracy, overall response time, differential response time for 'same' and 'different' responses, and differential response time for correct and incorrect responses. Patterns of responses by both subjects and our proposed model closely match responses observed on the Stroop and Flanker tasks. This suggests a re-interpretation of those classic tasks in which they require *information integration* with informative priors, providing a quantitative and principled way of understanding traditional notions of cognitive control and pre-potent responses.

4.3 Methods

We performed a variant of the N-back task with $N = 1, 2, 3$. After passing a color vision test and demonstrating an understanding of the task by reaching a performance threshold, each subject was presented with 18 experimental blocks of 70 images each. Data were collected from 26, 26, and 31 subjects for $N = 1, 2$ and 3, respectively. Following the task, subjects took a short version of the ICAR cognitive diagnostic test [61]. Data were collected via Amazon Mechanical Turk [62]. Subjects were financially compensated for their participation and were notified that they would be compensated at a rate corresponding to their performance in the task, relative to performance of other subjects. The research protocol was approved by the University of Minnesota IRB.

4.3.1 Stimulus design

Stimulus blocks were of two types: random and patterned. In random blocks, the sequence of target responses 'same' (S) and 'different' (D) were drawn from a categorical distribution with equal probability, with S and D indicating that the currently presented stimulus is the same as, or different from, the stimulus shown N trials previously. In the patterned blocks, the sequence of responses was constructed to contain *regularity*: roughly 94% of target responses followed the pattern $SDSDSD...$, with about 6% of target responses deviating from that pattern. Each subject was presented with 12 patterned blocks and 6 random blocks, randomly ordered. Critically, subjects were not told that there were two types of stimulus blocks, nor that different blocks were structured differently. Each block appeared visually identical to the others.

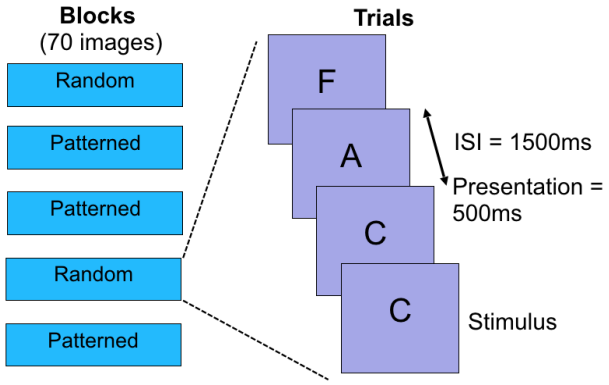


Figure 4.1: Diagram of stimulus sequencing. Following training, 18 blocks were presented composed of 70 images each. Each block was either 'random' or 'patterned'. Random and patterned blocks were randomly ordered.

To construct each stimulus block, we began with a 2-period sequence of responses $SDSDSD...$ for each block, such that each sequence was 70 trials long. For random blocks, 35 trial indexes were randomly chosen, and each sampled response was switched to the opposite response (D to S, for example), converting the sequence into a random sequence of responses. For patterned blocks, we performed the same operation on only 6% of the target responses, leaving the repeating $SDSDSD...$ sequence largely intact.

Once the target responses were constructed, the first $N-1$ stimuli were sampled with uniform probability from a vocabulary of 20 letters from the Romantic alphabet, including all of the consonants except for X[1]. Starting with the letter at index N and continuing to the 70th letter in the sequence, each letter was set to be the same as the target letter if the corresponding target response was S, otherwise it was sampled randomly from the vocabulary exclusive of the target letter.

At the beginning of the experiment, subjects were directed to a video detailing task instructions. Subjects were also presented with brief textual instructions at the beginning of each block. Subjects pressed a key to begin each block, and were permitted to rest between blocks. Once a block began, subjects also saw a short reminder of task instructions.

[1]D was unintentionally excluded from the 1-back, so the vocabulary had a cardinality of 19 in that case

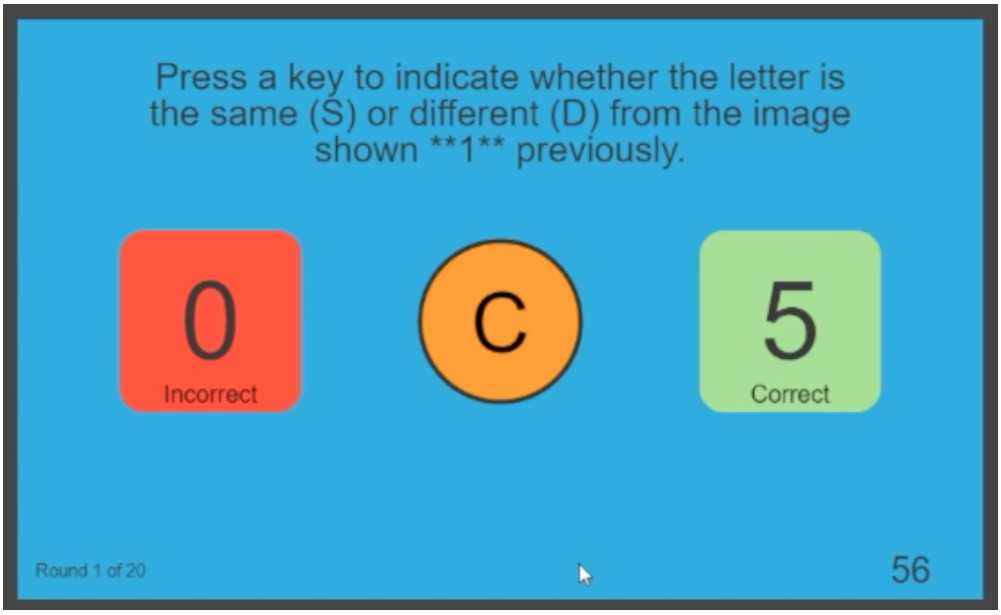


Figure 4.2: An example stimulus screen. The current letter appeared in the center of the screen. Instructions remained at the top of the screen for the duration of the experiment. Correct responses were tallied on the right, and incorrect responses on the left. Following each block, subjects saw a summary screen reporting their percent correct for that block. Patterned and random blocks appeared visually identical.

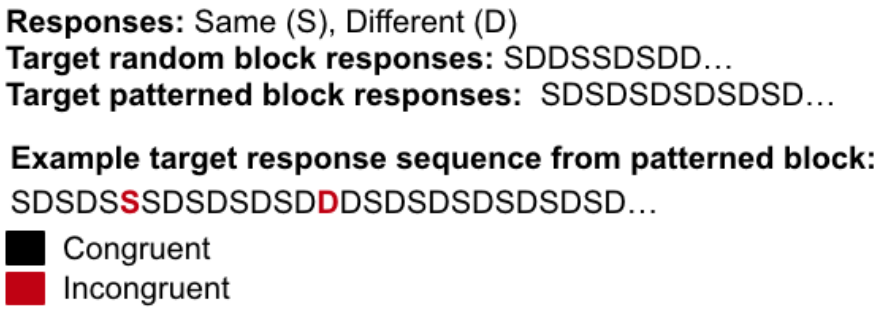


Figure 4.3: Response sequencing in random and patterned blocks. In random blocks, S and D responses are randomly ordered. In patterned blocks, responses typically follow a periodic pattern. Exceptions to this pattern are called incongruent trials, because the response is incongruent with the established sequential pattern.

The duration of each trial was 2000ms. Each letter was presented on the screen for 500ms, followed by a 1500ms delay. Subjects responded to each stimulus by pressing the S or D keys on the computer keyboard, and received feedback indicating whether each response was correct or incorrect. If a subject did not respond by the time the subsequent stimulus appeared, the response was counted as 'incorrect' and the trial was marked as 'skip'. During each block, a scoreboard was visible on screen containing the tally of correct and incorrect responses for the current block. A screenshot of the stimulus screen is shown in Figure 4.2.

4.3.2 Stimulus analysis

Trials in random blocks were designed such that the each response was equally likely, with the intention that subjects must remember past images in order to generate correct responses. We call trials in this condition 'neutral' in analogy with the neutral condition in the Stroop task, as there is only one stream of information available to the subject that is useful for generating accurate responses, aside from knowledge that each response is equally likely.

In patterned blocks, trials are divided into congruent and incongruent trials, again in analogy with the Stroop task. In congruent trials, the response produced by following the N-back instructions and comparing the letter on screen with the letter presented N trials previously are the *same* as the response that would be produced if the subject merely followed the repeating $SDSDSD...$ pattern present in the majority of the block. In incongruent trials, the response pattern is violated. In each incongruent trial, responding according to the repeating pattern produces an incorrect response, while responding according to the N-back instructions still produces a correct response. An example of congruent and incongruent trials is illustrated in Figure 4.3.

'Lures' are past stimuli that match the image currently visible but appear at $N-1$ or $N+1$ positions back [47]. When the stimulus at N is different than the currently visible stimulus, a lure trial can induce subjects to produce a response of 'same' at a rate greater than chance [45]. Roughly 5% of trials in the generated stimulus were lure trials of type $N-1$ or $N+1$.

4.4 Results

4.4.1 Main effect

This experiment was designed to assess whether subjects exploited statistical regularities in task stimuli and past responses to generate responses. To the extent that this is so, we expect subject error rates and response times to differ between 'patterned' blocks and 'random' blocks. As described above, 'patterned' blocks can be grouped into 'congruent' and 'incongruent' trials, in which statistical regularity either reinforces or contradicts the response predicted by the N-back instructions alone. Classic results from the Stroop and Flanker tasks suggest that congruent trials will produce faster response times and a lower error rate, while incongruent trials will generate slower responses and more errors, when compared to the random condition.

Statistical tests in the text were performed as follows. For each comparison described below, we calculated the accuracy and mean response time per subject per condition. We then took within-subject differences of accuracy and or response time between conditions, performed a bootstrap estimate of the mean of the difference, and computed the proportion of bootstrap samples on the other side of zero from the direction of the average difference. This method produces a bootstrap estimate of the likelihood that the observed comparison can be attributed to chance, summarized by a p-value.

Accuracy by subject for each trial type is shown in Figure 4.4, with subject accuracy on congruent and incongruent trials compared to accuracy on neutral trials. For the 1- and 2-back tasks, subjects almost universally exhibit higher accuracy on congruent and lower accuracy on incongruent trials with respect to neutral trials. The mean increase in accuracy across subjects from the incongruent to the random condition, and from the random condition to the congruent condition, are highly statistically significant ($p < 10^{-6}$). The trend is also present for some subjects on the 3-back task, though it is not present for subjects achieving high accuracy on neutral trials.

Subject response times are shown in Figure 4.5. Again we see a robust effect of trial congruence and incongruence when compared to neutral trials. In 74 out of 83 subjects (89%), incongruent trials take longer, on average, than congruent trials, and the mean within-subject change is highly significant ($p < 10^{-6}$). All but one of the subjects who do not follow this trend were performing the 3-back task, for which we see

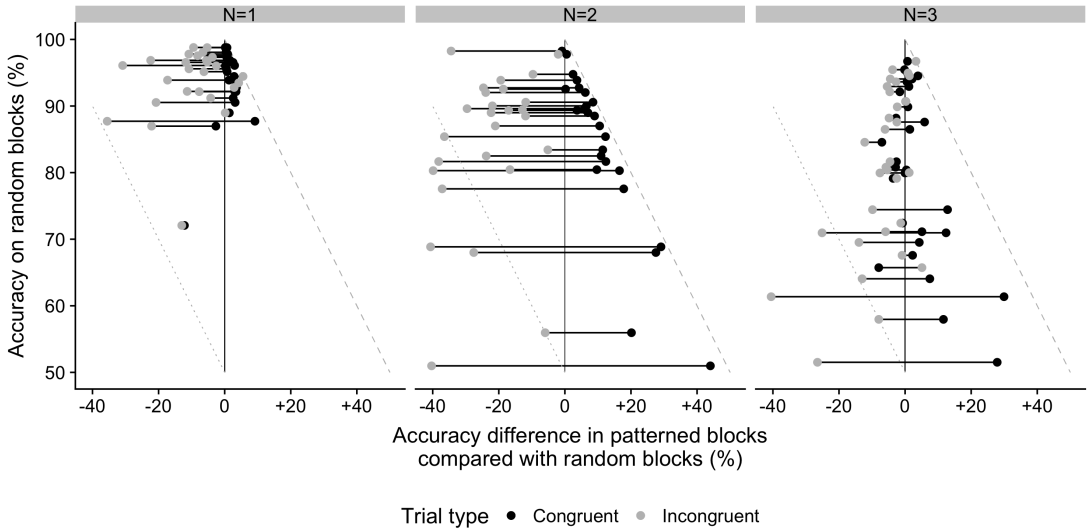


Figure 4.4: Response accuracy in congruent and incongruent trials. Each subject is represented as a line connected by two dots. Accuracy on congruent and incongruent trials is expressed in relation to accuracy on neutral trials. The vertical black lines represent a 0% accuracy difference from neutral trials. The gray dashed line demarcates the achievable region, and the gray dotted line represents chance performance. Accuracy is higher in the congruent than the incongruent condition ($p < 10^{-6}$), higher in the congruent than the random condition ($p < 10^{-6}$), and higher in the random condition than the incongruent condition ($p < 10^{-6}$). Significance tests are described in the text.

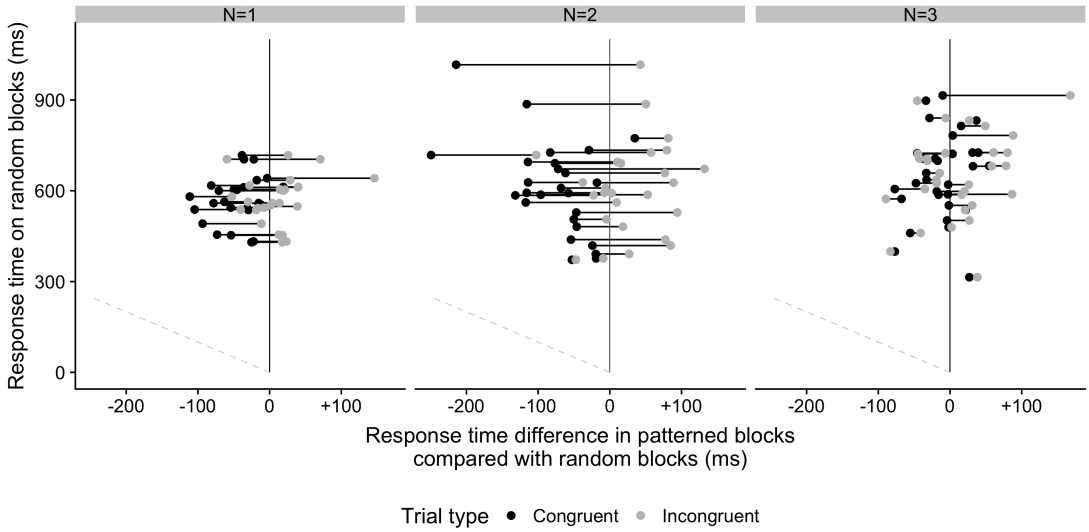


Figure 4.5: Mean response time for each subject. Each subject is represented as a line connected by two dots. Response time on congruent and incongruent trials is expressed in relation to response time on neutral trials. The vertical black lines represent response time difference, and equivalent performance in each case would be evidenced by dots lying on the black line. The gray dashed line demarcates the achievable region. Both correct and incorrect responses are represented in the response time mean for each subject, though no-response trials are omitted. Subject response times decreased in the congruent condition compared to the random condition ($p < 10^{-6}$) and the incongruent condition ($p < 10^{-6}$), and decreased in the incongruent condition compared to the random condition ($p < 0.001$).

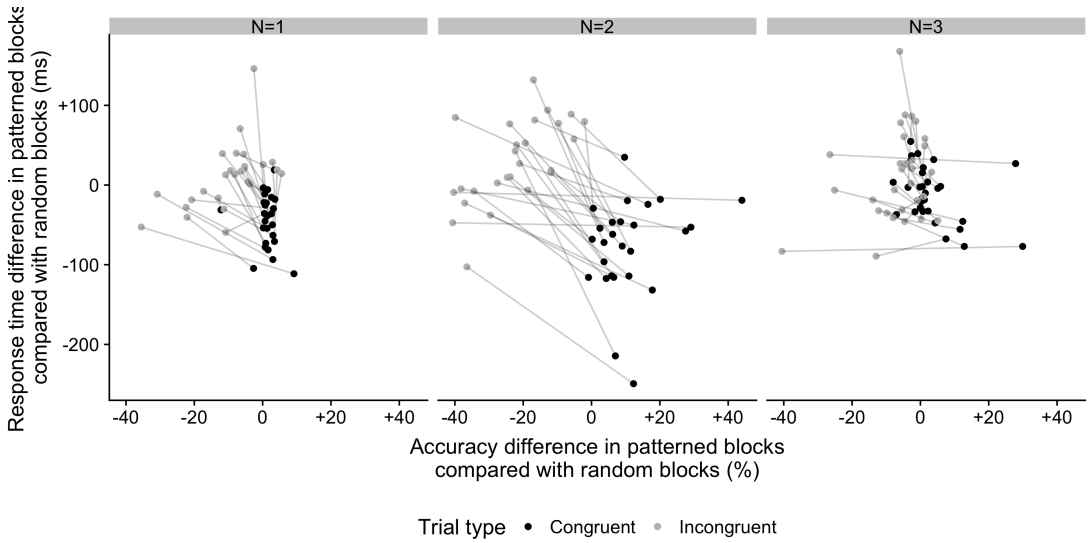


Figure 4.6: Subject accuracy and response time differentials plotted by subject.

higher variation in behavior.

A combined accuracy and response time plot is given in Figure 4.6. The congruent and incongruent conditions are linearly separable for $N = 2$, nearly so for $N = 1$, and more variable for $N = 3$. For the $N = 3$ condition, subject behavior is more variable, though most subjects do show either a change in response time or accuracy that is consistent with the other values of N.

Taken together, analysis of subject response time and accuracy for congruent and incongruent trials reveals patterns of behavior strongly consistent with behavior in the Stroop and Flanker tasks. On the whole, congruent trials shorten response times and increase accuracy, and vice versa for incongruent trials, with respect to neutral trials.

Results clearly suggest that the majority of subjects combine information from multiple sources rather than using any source exclusively. If subjects exclusively followed the N-back task instructions and utilized only their declarative memory of past stimuli, exploiting no statistical regularity in stimulus or responses, we would expect responses on both congruent and incongruent trials to have the same time and accuracy characteristics as neutral trials – as from the perspective of the subject, these trials would be no different from neutral trials. However, a large and statistically significant difference

is present. Moreover, if subjects exclusively utilized the regularity present in patterned blocks, we would expect 100% accuracy on congruent trials and 0% accuracy on incongruent trials. This is also clearly not the case. Taken together, this represents strong evidence in favor of the hypothesis that subjects are *combining* information from multiple sources to generate responses on the N-back task. Implications for interpretations of the task are considered in the discussion, below.

4.5 Information transmission model

In concert with the remainder of this dissertation, we seek to understand the normative constraints on information transmission involved in performing this task. In this section, we show that consideration of these constraints produces response characteristics that match human behavior in both the main congruence/incongruence effect and several auxiliary behavioral effects. We first briefly recount the information transmission model detailed in Chapter 2, and describe its application to the modified N-back task. We then simulate task performance using the information transmission scheme, and compare simulated performance with human data.

In Chapter 2, we describe an information transmission scheme in which symbols are encoded into firing rates of an array of Poisson processes (Figure 4.7). An ideal observer counts the sequences of spikes produced and continuously infers the underlying rate configuration of the Poisson processes. The observer tracks the entropy of the posterior distribution over source configurations, and transmission occurs until an entropy threshold is reached and an action is taken.

In each trial of the N-back task, subjects observe a letter and construct a response. In the framework of the information transmission model, the stimulus on the screen is the transmitted stimulus, encoded into an array of Poisson spikes. The receiver decodes which letter is being transmitted. In a simple stimulus-response task, like those used by Hick and Hyman [2, 3], each stimulus corresponds to a separate action. In the N-back task, however, an additional step is needed to compute the appropriate action given a decoded stimulus: as the letter is decoded, a posterior over likely actions is also maintained and updated in real time. An action is taken when an entropy

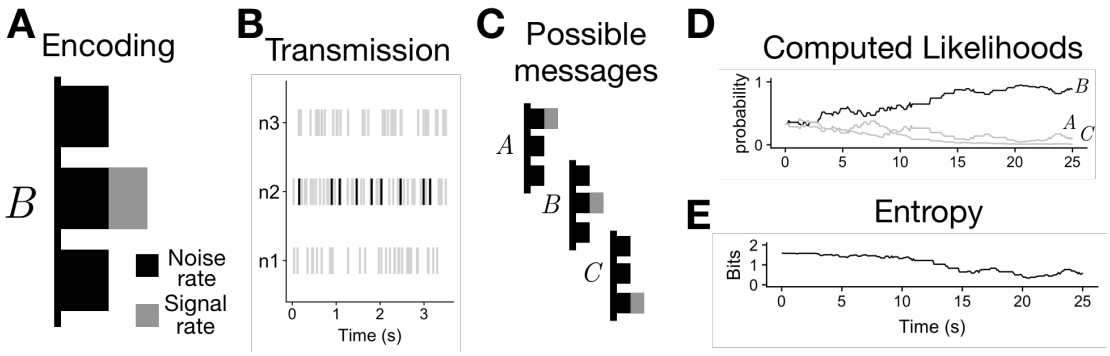


Figure 4.7: Schematic of the information transmission model described in Chapter 2. (A) A symbol is encoded as a vector of Poisson process firing rates, which produce a sequence of spikes shown in (B). (C) The decoder maintains a codebook of possible messages and their corresponding source rates. (D) The decoder computes likelihoods of each source configuration having produced the observed spikes, and combines the symbol-wise likelihoods with a prior probability over symbols to produce a posterior distribution. (E) The entropy of the posterior distribution is tracked and the symbol is 'decoded' when the entropy reaches a threshold. The entropy is calculated using the posterior distribution over symbols, which combines the likelihoods from (D) with a prior distribution representing expected symbol frequency.

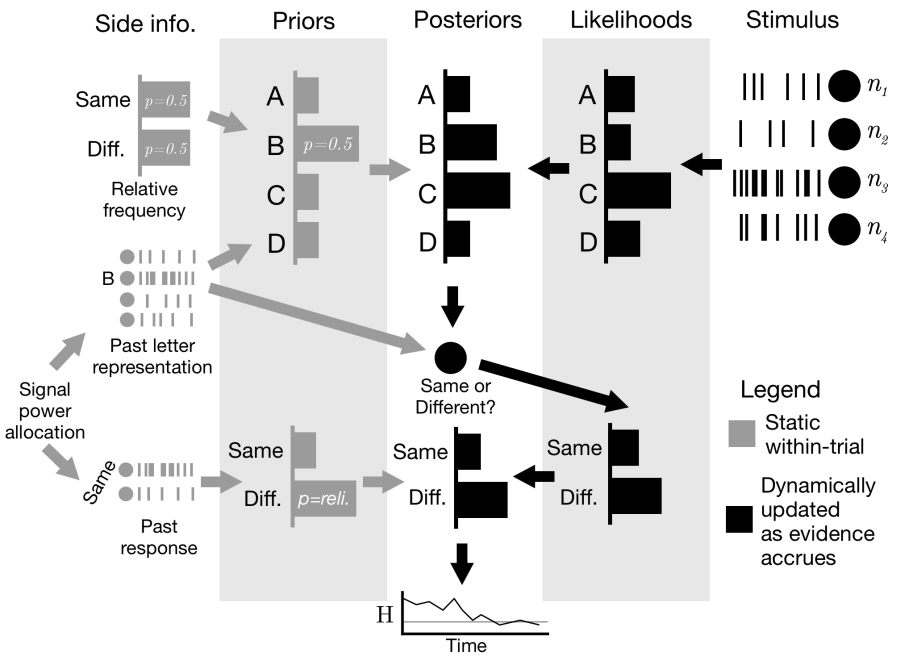


Figure 4.8: A schematic of the combining of information in order to generate a response. On the left side, under 'Side info,' information about past responses, past observed letters, and the baseline rate of 'same' vs 'different' responses is encoded into priors over future stimuli and actions. On the right, under 'Stimulus', an observed stimulus is converted to a likelihood over letters, which is combined with prior information to create a posterior distribution over letters (top center). This posterior is combined with both previously observed letter to produce a likelihood of 'same' or 'different' response. The response likelihood is combined with the prior response to create the posterior over responses. The entropy of the response posterior is tracked until it reaches a pre-set threshold (bottom center), at which time action is taken according to the action corresponding to the highest probability mass. The effect of image and action prior strengths on simulated response behavior is illustrated in Figures 4.12 and 4.13.

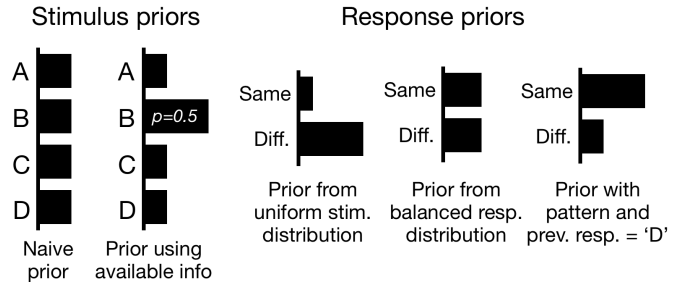


Figure 4.9: Statistical information is used to construct informative priors for stimuli and responses. Various prior distributions generate very different simulated behavior, as illustrated in Figures 4.12, 4.13, and 4.14.

threshold is reached *for the distribution over actions*. A schematic of the stimulus-to-action information flow is given in Figure 4.8.

The variable-length transmission model of the N-back task provides an explicit place for information about previously observed letters, the relative frequency of responses, and statistical patterns in target responses to influence responses: decoding priors. A prior distribution over responses is provided by the statistical structure of responses. On random blocks, S and D have equal frequency and result in a uniform distribution over responses, while in patterned blocks the response prior is (or at least, can be) heavily biased towards the response opposite to the previous response. Knowledge of previous stimuli can also influence priors over stimuli. Knowing that the letter A was observed previously, and that half of trials have a response of 'same', an ideal observer would place $p = 0.5$ on the next letter being A, while the remaining probability mass would be distributed over the remaining letters.

The key insight provided by the variable-length transmission model of the N-back task, and the one that explains the observed behavioral phenomena, is that response time is directly related to the quantity of information transmitted from the stimulus, through the nerves and brain, and to the fingers – and this quantity is influenced by subject prior distributions over both stimuli and responses. Recall that from the perspective of the decoder, information transmitted is equivalent to the KL-divergence between a prior distribution (over stimuli and over responses) and a posterior distribution over the same quantities [20] at response time (see Chapter 3 for further discussion). As

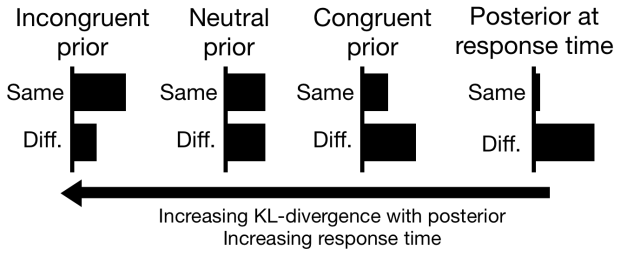


Figure 4.10: The relationship between the prior distribution and the posterior distribution required for a response determines response time. Incongruent priors have larger KL-divergence with the posterior at the entropy threshold than congruent priors, leading to larger response times.

side information impacts the prior distribution over both the stimulus observed and the likely response, it also influences the amount of novel information that must be integrated on each trial before an entropy threshold is reached and a response is generated, and thus influences the response time. In most cases, prior information aids subject responses by capturing information that would otherwise need to be decoded from the environment. 'Congruent' trials are an extreme case of this. In other cases, prior information contradicts information from the environment, creating 'incongruent' trials. Since information transmission time is related to response time (see Chapters 2 and 3), such prior congruence and incongruence with stimuli and responses directly influences response times in a predictable way. The strength of the priors shown in Figure 4.8 affects the relative response times for congruent and incongruent conditions, 'same' vs 'different' targets, and correct responses vs errors.

4.6 Simulation results

Using the information flow pattern outlined in Figure 4.8, we simulated responses to stimuli under congruent, neutral, and incongruent conditions under a range of entropy thresholds, signal powers, and noise powers. Unless otherwise noted in the figure caption, simulation results represent a range of parameters whose response time and accuracy results are roughly compatible with behavioral observations. Simulation results are plotted in Figure 4.15 in a format consistent with the experimental results shown in

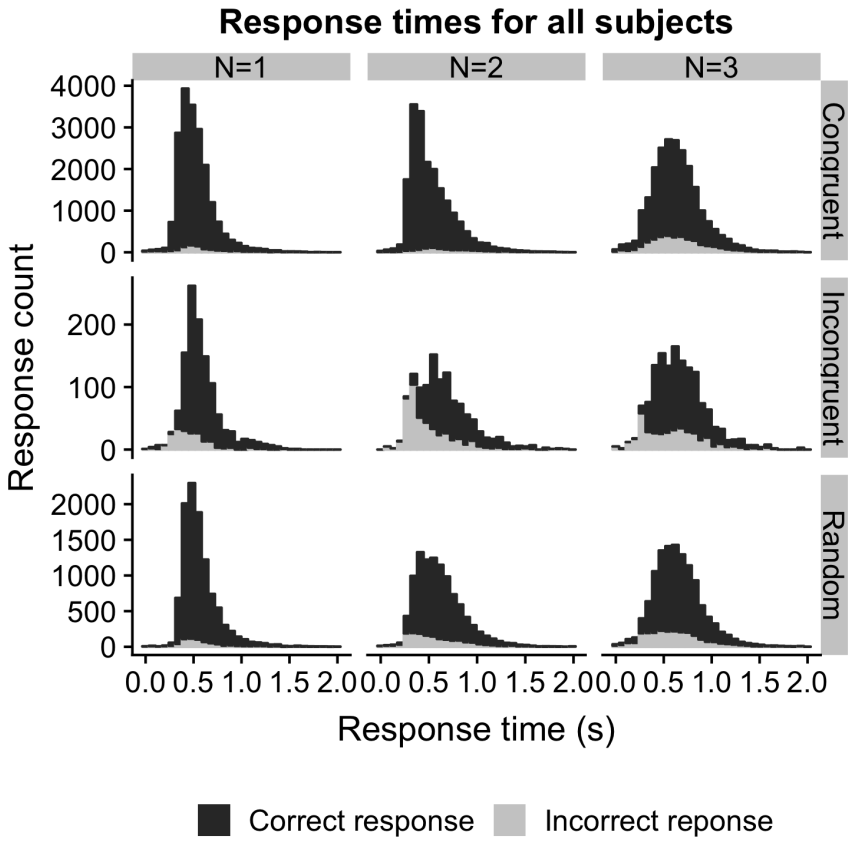


Figure 4.11: Distributions of subject response times by values of N and condition. Data from all subjects is pooled. Incorrect responses tend to be faster than correct responses, particularly for the incongruent condition. Compare to Figures 4.12 and 4.13.

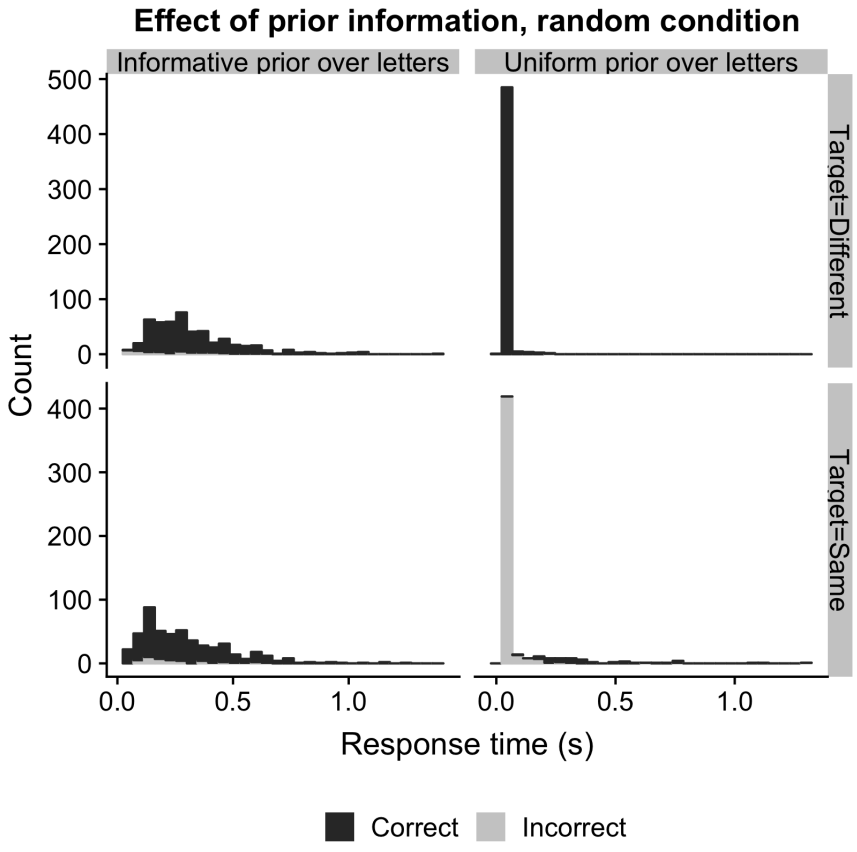


Figure 4.12: Simulated response times with both an informative prior over letters (see Figures 4.8) or a uniform prior over letters, as pictured in Figure 4.9. Signal power and noise power were both 15 spikes/second, with an entropy threshold set to 0.5 bits. Placing a uniform prior over letter stimuli results in very fast responses, and almost all responses for a target of 'same' are incorrect. Compare with human data in Figure 4.11.

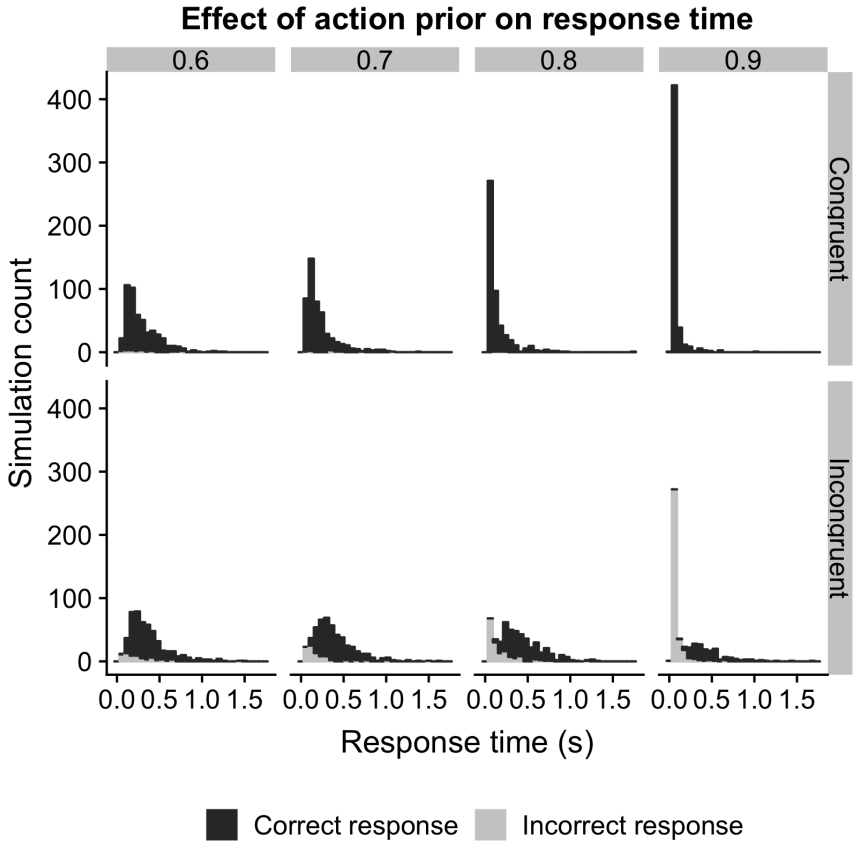


Figure 4.13: Simulated response time distributions for various weightings of previous responses, corresponding to the $p = reli.$ in the response prior in Figure 4.8. Simulations were performed with a signal and noise power of 15 spikes/second, with an entropy threshold of 0.5 bits. Comparing with human results in the Congruent and Incongruent conditions in Figure 4.11, a prior weight of about 0.7 matches human data.

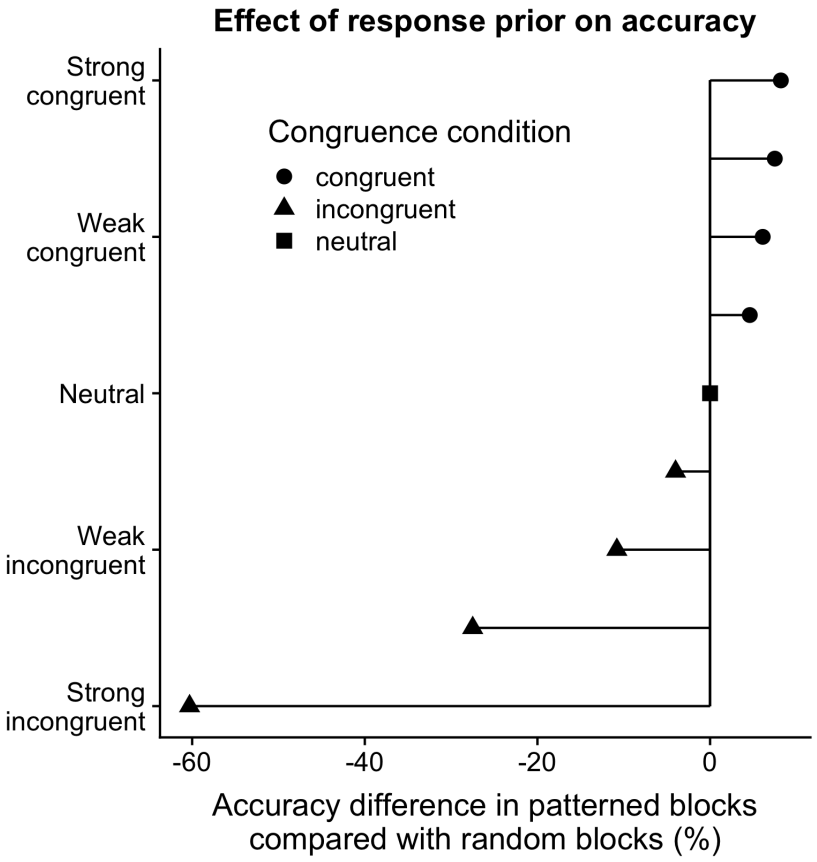


Figure 4.14: Accuracy of simulated trials is strongly affected by the strength of the response prior. In each case, simulations were performed with an entropy threshold of 0.5 bits, and both signal power and noise power of 15 spikes/second. Prior information creates characteristic errors for the incongruent condition, and increases accuracy for the congruent condition.

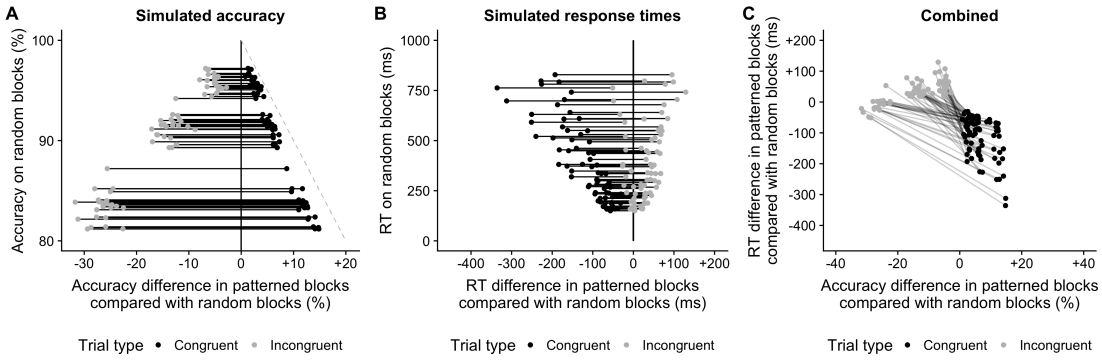


Figure 4.15: Simulated message transmissions under congruent, neutral, and incongruent conditions for a range of signal powers, noise powers, and entropy thresholds. Congruence reflects the relationship between the response prior ('same' or 'different') and the target response. All congruent and incongruent transmissions were performed with a 'reliability' value of 0.7, which represents a medium-strength prior over responses, while neutral transmissions reflect a 'reliability' value of 0.5. Each point is a summary of 500 simulated transmissions. Compare with human responses in Figures 4.4, 4.5, and 4.6.

Figures 4.4, 4.5, and 4.6. Similar to human subjects, simulations show faster response times and lower error rates with congruent trials when compared to neutral trials, and the pattern is reversed for incongruent trials.

Interestingly, simulations reveal that accuracy can be manipulated in a predictable way by manipulating the prior on responses. Generally speaking, a fixed stopping threshold on entropy translates to a fixed value for response accuracy: a lower entropy threshold results in high accuracy, and vice versa. However, a prior belief in a given response appears to induce a corresponding bias in responses, increasing accuracy when the prior and correct response are congruent, and decreasing accuracy when they are incongruent. This can be seen in Figure 4.15: each horizontal line represents a single fixed set of simulation parameters, including a fixed entropy stopping threshold. Despite this, varying the prior distribution over stimuli and responses produces variation in error rates. This effect can be explained by the fundamental difference between decoder entropy over the action posterior distribution, a fundamentally subjective quantity, and accuracy, which is objective. That subjects exhibit the same pattern of responses in Figures 4.4 and 4.5 provides further evidence for the suggestion that responses are

influenced by priors over responses.

Responses of 'same' vs 'different'

In addition to the effects of stimulus congruence and incongruence on response time and accuracy, subjects typically respond more quickly when the presented stimulus is the same as the stimulus presented N previously than they do when it is different ($p < 0.001$). Average response times by subject are shown in Figure 4.16. This difference in response time by target response is also replicated by our model, as illustrated in the figure. The shape of the prior distribution over letters, with a larger weight placed on the 'same' response shown in Figures 4.8 and 4.9, is critical to replicating this effect in our model. Placing a uniform prior on images results in much faster simulated response times for 'different' than 'same' responses. This does not match human behavioral data.

Response time distributions

The full distribution of pooled subject response times separated by congruence condition is given in Figure 4.17. As shown in the summary figures above, subjects tend to respond more slowly with higher N. The effect of congruence or incongruence is also evident, with congruent responses faster than neutral responses ($p < 10^{-6}$), and neutral responses faster than incongruent responses ($p < 0.005$), on average. Viewing the full response time distribution shows that the effect is relatively small when compared to the variation in response times.

Response times for simulated transmissions are illustrated in the bottom two panels of Figure 4.17. Simulated response times are distributed in a way qualitatively similar to human responses, though they begin near 0ms rather than 200ms. Distributions are shown for two values of transmission noise power, with only the lowest simulated value for signal power. The shape of the plots suggest that human responses are most similar to simulations with a relatively low signal-to-noise ratio (SNR).

Separating responses by correctness (see Figure 4.18) reveals that the relationship between response times on congruent, neutral, and incongruent trials is reversed when errors are committed. In this case, subjects respond most quickly to incongruent trials, followed by neutral, followed by congruent (all significant at $p < 10^{-4}$). The ordering holds for each level of N, and is also exhibited by the model. This pattern occurs

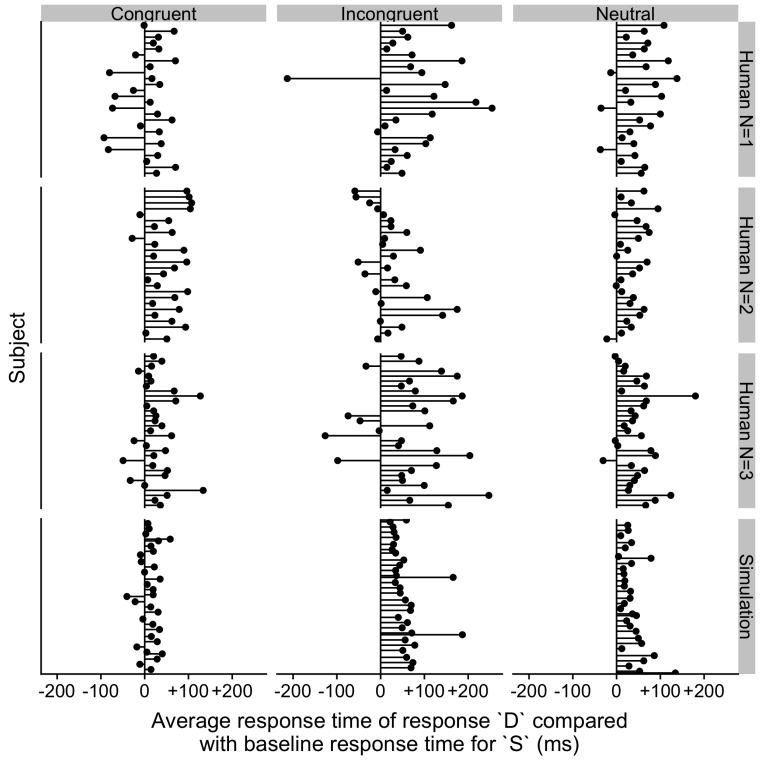


Figure 4.16: Comparison of average response times on 'same' and 'different' trials for each subject, and for simulated transmissions. The average difference in response time for 'different' vs 'same' is plotted relative to 0, where an identical value would result in a point on the vertical line. Subjects and simulations largely exhibit slower responses when the target response is 'different' vs when it is 'same' ($p < 0.001$). Simulations suggest that this effect is largely due to the shape of the prior distribution over stimuli, as discussed in the text.

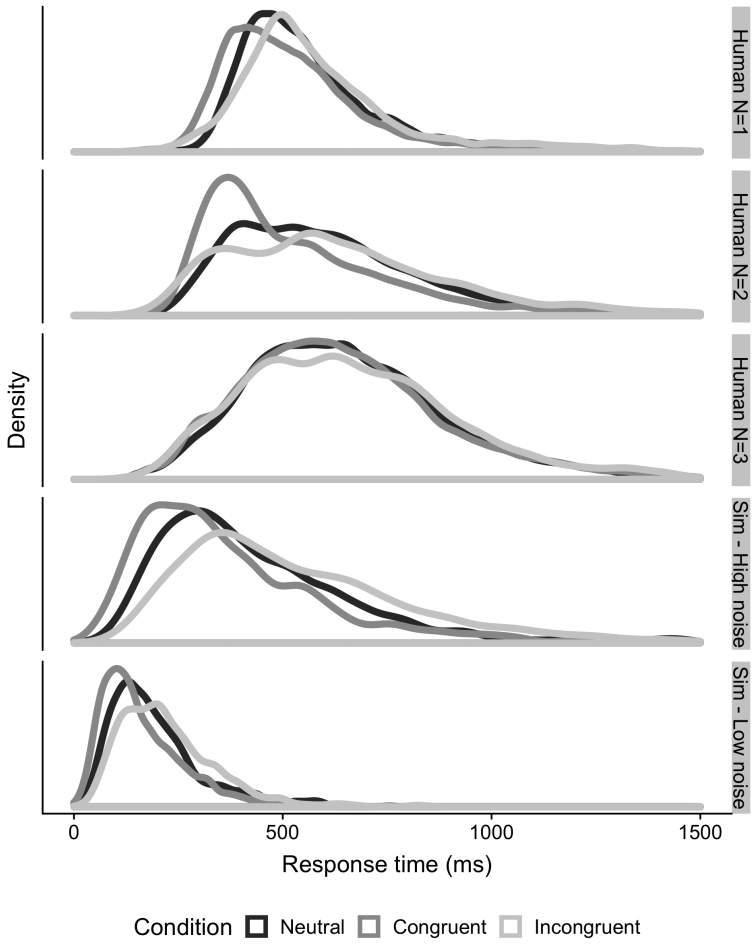


Figure 4.17: Distribution of pooled response times across subjects for each value of N, and for two simulations. The distribution of subject data more closely resembles the high-noise simulation. For each condition, responses on congruent trials are faster than responses on neutral trials ($p < 10^{-6}$), which are faster than responses on incongruent trials ($p < 0.001$).

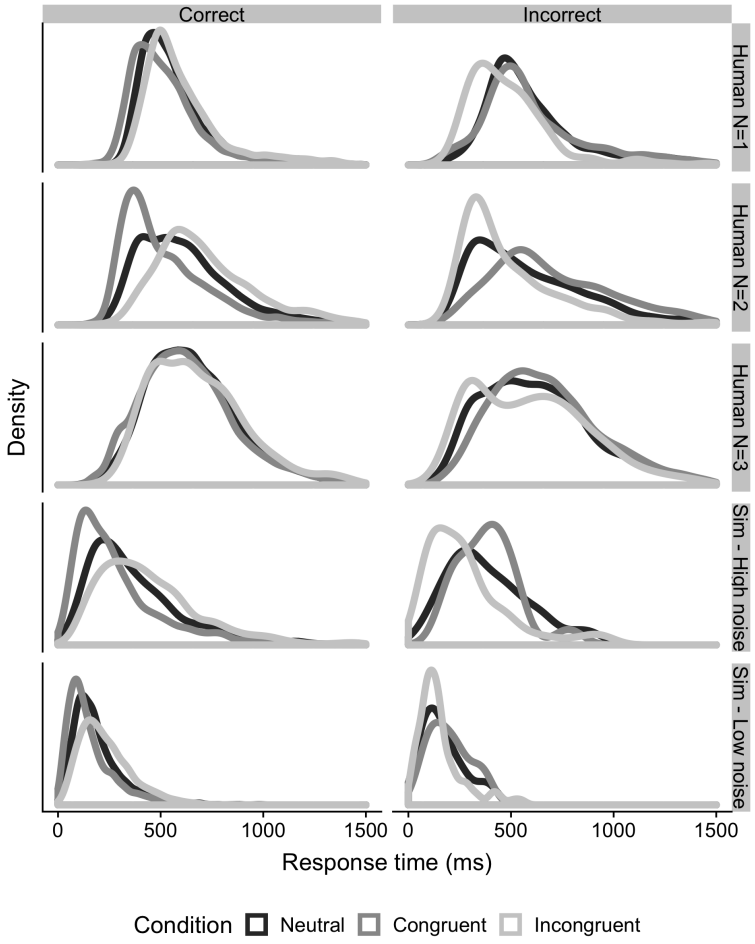


Figure 4.18: Response times pooled across subjects and faceted into 'correct' and 'incorrect' responses. While correct responses show the expected ordering of incongruent, neutral, and congruent response times, the pattern is reversed for incorrect responses, and the differences are statistically significant ($p < 10^{-4}$). This reversal is also present in simulation results.

because the condition labels *congruent* and *incongruent* indicate that the response is biased towards a particular response, where the bias is encoded in the strength of the prior over responses. The KL-divergence between the prior and the 'biased-towards' response is therefore relatively small, and might be overcome by channel noise.

4.7 Discussion and implications

We found that subject response time and accuracy on the N-back task is influenced in a predictable and consistent way by the statistical structure of task responses. This finding supports skepticism over whether the N-back task exhibits construct validity as a purely working memory task [47, 45], as subject behavior appears to combine and weight information from multiple sources that include response statistics in addition to properties of the stimulus. The N-back task continues to serve as an interesting and useful experimental paradigm, but our findings add to the growing chorus of suggestions that the stimulus should be carefully constructed and its statistics checked for unintended regularity and structure.

We showed that the influence of experimental manipulations on subject behavior was well-modeled by a continuous information transmission model in which stimulus regularities are represented by the shape of the prior used by the receiver to decode the transmission of stimulus content and convert it into action. The close match between model and subject behavior lends weight to the idea that perception is Bayesian [63], exploiting prior information to speed recognition and increase its accuracy. That prior information is critical to modeling subject responses is consistent with recent work demonstrating Bayesian information integration into motor responses in more complex movement tasks [64].

We demonstrated in Chapters 2 and 3 that the Bayes-Poisson signal transmission model accounts for several classic findings in behavioral psychology, including the Power Law of Learning [18] and the Hick-Hyman law [2, 17]. While this parsimony is desirable in-and-of itself, the scientific value of a model lies in its ability to make testable predictions and explain novel findings. In this chapter, we have shown that the model predicts and accounts for the effects of the statistical structure of both task stimuli and responses on both subject response time and accuracy in a principled and interpretable

way. The model also correctly predicts the response time differential between 'same' and 'different' responses, and the way in which the response time patterns vary with error responses vs correct responses. We suggest that this represents a major validation of the modeling strategy as an algorithm-level model of cognitive processes involved in responding to stimuli.

4.7.1 Limitations

There are several opportunities to extend the work presented here. Perhaps most importantly, we do not yet possess a closed-form relationship between model parameters (like signal power, stimulus cardinality, and entropy threshold) and subject behavior in the form of expected response time and error rates, as mentioned in Chapter 2. With a closed-form relationship between parameters and data, we would be able to infer individual subject parameters, study individual differences, and perform principled model comparison with alternative explanations.

In addition, there are several improvements in the experimental design that should be implemented in future work. In the current design, each subject only completed the experiment for a single value of N. Collecting data on several values of N for each subject would allow a comparison of inferred model parameters with subjective effort. Recent work has shown that subjects find the N-back task increasingly aversive as N grows [65]. It would be valuable to investigate associations between subjective change in effort expended and model parameters such as signal power or noise power. For example, does effort map to increased signal power, or to inference in the presence of greater noise?

Collection of data on Amazon Mechanical Turk also presented several unexpected challenges. Subject attrition was high (around 50%). It is possible that voluntary attrition may have biased results to exclude subjects for whom the N-back task was unpleasant or particularly difficult, or some other unmeasured confound. This possibility has only minimal impact on the current analysis, as all analyses were either within-subject or within-condition, but it would be a problem were we to attempt to perform analyses across values of N.

Finally, the period-2 response pattern in the 'patterned' condition induced a statistical regularity of the stimuli in the 2-back task that was not present in the 1- or 3-back

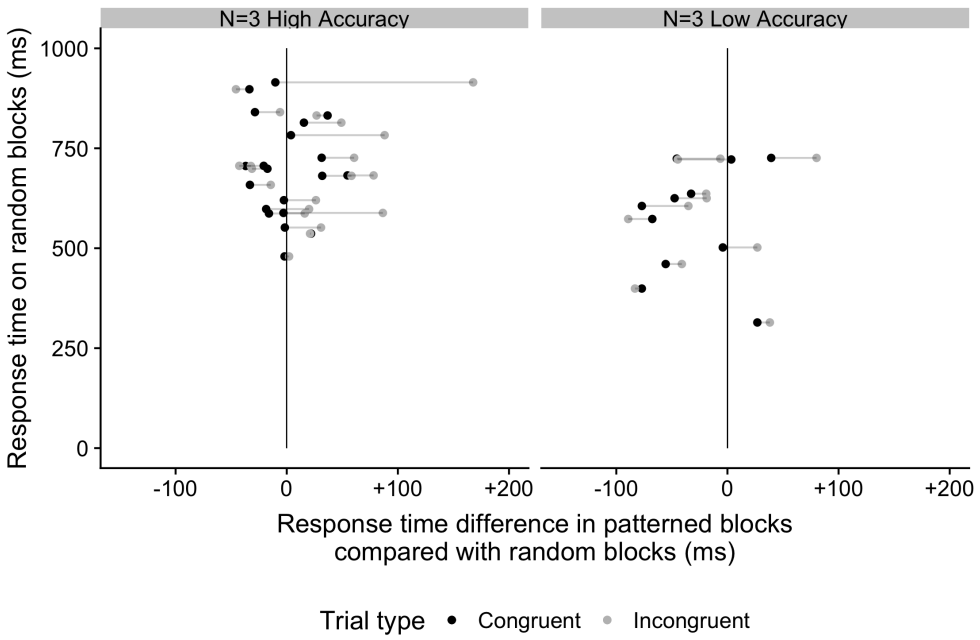


Figure 4.19: Average response times by congruence condition on the 3-back task, separated by whether subjects achieved high accuracy (defined as accuracy $> 75\%$) or low accuracy. As shown in Figure 4.4, high accuracy subjects on the 3-back task showed very little sensitivity to congruence condition in terms of accuracy. The effect of congruence condition on response times is relatively robust.

tasks, and may explain why the effect of congruence and incongruence was stronger than for the 2-back task than the 1- and 3-back. The existence of this regularity can be subsumed by the prior over letters, so it does not invalidate our analyses or conclusions. Nevertheless, it represents an undesirable source of statistical variation across N-back conditions.

4.7.2 The 3-back puzzle

Some subjects performing the 3-back task exhibited qualitatively different behavior than subjects performing the 1- and 2-back tasks. In particular, Figure 4.4 shows that subjects with high accuracy on the 3-back task show very little sensitivity to statistics in the responses, that is, of congruence or incongruence in trials. We consider two

possible explanations for this phenomenon. First, it is possible that some subjects performing the 3-back task are extremely high achievers and value accuracy highly. Many (but not all) of these subjects exhibit the expected change in response time as a function of congruence condition, as illustrated in Figure 4.19. We divided subjects into 'high accuracy' and 'low accuracy' groups, where high accuracy groups achieved $> 75\%$ accuracy on the random condition, and plotted their response times. The high accuracy group showed slower response times (145ms slower on average), indicating that they may have prioritized accuracy over speed in the task overall, and *also* with respect to the influence of the congruence condition. An argument against this hypothesis is that subjects who maintained high accuracy (and thus a low entropy threshold) on the 1- and 2-back tasks nevertheless exhibited a relatively high sensitivity to congruence conditions in terms of response accuracy, as did the simulation results with a pre-specified low entropy threshold.

An alternative explanation is that subjects who perform with high accuracy on the 3-back task are *unaware* of the presence of a pattern in the target responses, or are unwilling to invest cognitive resources in tracking an unreliable auxiliary source of information. The patterned response leads to correct responses for the vast majority of trials in patterned blocks, but not every trial. Perhaps risk-averse subjects, or subjects who highly prioritized accuracy, were not willing to incorporate an unreliable signal. One of these proposals might explain why approximately 10 out of the 20 high-accuracy 3-back subjects showed no statistically significant effect of condition on response time, whereas only 2 of 11 low-accuracy showed no effect.

Considering the model itself, suppose the statistical information about the task is maintained not as an abstract prior distribution, but instead as a recurrent spiking network that utilizes resources in the maintenance of the representation. In a limited-resource environment, an agent would need to allocate resources (perhaps an overall spike rate) to maintaining prior information or transmitting information about the stimulus. In a high-demand task, this could manifest as a sub-optimal combining of information: either the subject relies heavily on the prior, in which case we would see an extreme effect of the congruence condition, or relies heavily on updating the likelihood and ignores the prior, leading to a diminished effect of the congruence condition.

This uni-dimensional allocation decision – maintaining the prior or updating the likelihood – might explain the grouping we see in the 3-back task, and the higher demands of the 3-back task might explain why it is only apparent there. More research is needed to investigate the relative merit of these possible explanations.

4.7.3 Conclusion

We have demonstrated that subject behavior on the N-back task is responsive to the statistical structure of both stimuli and responses in addition to past and currently viewed images as typically assumed by task instructions. We introduced a principled manner for combining information and showed that simulations matched human behavior in a range of characteristics, validating the information transmission model introduced in Chapter 2.

We also uncovered structural similarities between the N-back task and other cognitive control tasks. If stimulus congruence and incongruence with prior expectations can be so cleanly modeled in the N-back task, it raises the question of whether classic tasks like the Stroop, Flanker, and Stop-Signal tasks can be similarly modeled. If so, it would establish that our quantitative model of inference and information transmission is a parsimonious and valuable model for a range of tasks that currently have primarily qualitative explanations. It may be that classic concepts of priming, pre-potent responses and recency effects can likewise be formalized in inferential and information-theoretic terms.

Chapter 5

Why do some tasks feel more effortful than others?

5.1 Overview

Some tasks give rise to a subjective feeling of mental effort, while others do not. Existing literature on cognitive control addresses the decision of *whether* to engage in such tasks as a function of motivational incentives, by weighing mental costs vs intrinsic and extrinsic benefits. It is less clear *why* some tasks are more demanding than others in the first place, or why effort often decreases with practice. We propose that effort is a function of the energetic cost of encoding and transmitting task variables, and that this cost is itself a function of task exposure. Grounded in information-theoretic formalism, this model provides a normative explanation for mental effort, predicts a general lack of transfer learning, clearly distinguishes cognitive control from self-control, and provides a quantitative way to formalize task interference and pre-potent responses.

5.2 Introduction

We are all familiar with the feeling of mental effort and accumulating fatigue. We must concentrate to drive in heavy traffic or play a game of Go. It takes particular effort to learn a new skill or converse in a new language. The effort expended is not without consequence: we finish the game of Go exhausted, or slip back into our native

tongue when given the slightest encouragement. We may even decide that learning a new language is not worth the effort. What is it about the demands of these tasks that gives rise to the experience of effort? And why does that effort seem to decrease with practice?

As it relates to decision making and practice effects, mental effort has been thoroughly studied, though often by disparate communities of researchers. Behavioral economists have described our tendency to avoid mental effort via the use of 'fast-and-frugal' heuristics [66], and speak of a 'law of least mental effort' [67] leading humans to act as 'cognitive misers' [68]. Others have shown that the use of mental effort appears to be an active decision that is sensitive to extrinsic rewards, and that the reward required for a given level of effort expenditure varies across individuals [65] and with task demands [58, 65]. That mental effort requires incentivization is no surprise, as it also induces negative emotion [69, 70, 71], avoidance behavior [72, 65, 73], and a tendency to quit [74] or become fatigued [75, 76, 77]. Luckily, mental effort from task engagement can be reduced via practice: investigators of task 'automaticity' have observed that extensive practice with a task tends to decrease the effort required to perform the task [78, 26], possibly because the requisite computations begin as 'model-based' mental-simulation and settle into 'model-free' policy execution [79]. Furthermore, the rate of response time decrease with practice is consistent enough to warrant calling the trend a "Power Law of Practice" [80, 18].

The circumstances in which mental effort arises fall into four categories: tasks requiring a high level of attention or memory, novel tasks, tasks that introduce a conflict between a 'pre-potent' response and a 'correct' response, and frequent switching between tasks. It is not yet clear what these task types have in common that explains their giving rise to a common subjective experience of effort. More troubling, there is as yet no normative explanation for whether, and why, a given task will require mental effort, or the rate at which effort will decrease with practice. Attempts to describe effort reduction as a consequence of developing a 'model-free' state-action mapping [79] do not account for the fact that in many effort-inducing tasks, a policy is already provided to subjects in the form of explicit instructions. Literature on task automaticity characterizes the reduction of effort with practice, but efforts to provide normative predictions (rather than simply descriptions) of this effect are limited to memory retrieval and not

task performance per se [28, 81, 30]. Finally, despite the constraints inherent to any operation of a biological system, the nature and existence of a relationship between mental effort and biological constraints remains a matter of debate.

Our goal in this chapter is to argue that mental effort tracks the energetic costs of representing and transmitting task-related variables. Using the Bayes-Poisson model introduced in Chapter 2, we propose that in the cases of attention and working memory load, novel tasks, and conflicting tasks, mental effort tracks the number of spikes required to transmit task-related information. In novel tasks, we show that an inefficient and un-adapted code requires more Poisson spikes to transmit the same stimulus variables than an efficient code. We model conflict tasks, such as the Stroop task, with a leaky attentional filter, in which transmission noise slows response times and increases the number of spikes required to perform each trial of the task. Each case gives rise to mental effort, and each case uses energy (modeled as spikes) at a high rate. Viewing task costs through the lens of information transmission costs provides a unifying perspective that brings cohesion to the seemingly unrelated tasks associated with mental effort.

5.2.1 Background

What task conditions give rise to the experience of mental effort? Mental effort produced by tasks is typically ascribed to the intensive utilization of a constrained cognitive process. Sustained attention leads to mental effort and eventual fatigue, which is induced by so-called 'vigilance' or 'selective attention' tasks that require constant monitoring of a stimulus for an infrequent signal [82]. Tasks requiring use of famously-limited working memory resources, such as the N-back task, are also reliable and widely-cited drivers of mental effort. With working memory tasks, the experience of effort increases with memory load [65]. There is also a well-documented tendency to minimize load by leaving task-relevant information 'in the environment' when possible [83, 84, 85], and only refer to it as moment-by-moment task demands dictate. This suggests a pressure to minimize cognitive load *within* tasks, a tendency that has been associated with the use of heuristics [66] and cognitive biases [40].

Critically, it is not just attention or memory load that gives rise to a sense of effort. Another category of effort-inducing tasks introduces a conflict between two or more

response mechanisms. The famous Stroop task [9, 86] requires subjects to read a colored word and respond with the color of the word rather than its text - a difficult and fatiguing request to fulfill [87], that leads to frustration [88], negative affect [69], and a desire to quit [74]. Other conflict-inducing tasks include the Stop-Signal Task, in which subjects are instructed to respond in contradictory ways in rapid succession [89], and the Flanker task, in which a symbol is shown adjacent to other symbols that indicate incompatible responses [8]. A common interpretation of human performance in these tasks is that individuals have a 'pre-potent response' available for each stimulus that must be 'overridden' [90]. Responding in a manner incompatible with the pre-potent response is said to require 'cognitive control' [91] and use of 'executive function' [92], concepts which overlap heavily with attention and working memory utilization. While response incompatibilities within a task produce a feeling of effort, so do incompatibilities in temporally adjacent tasks. Experimental paradigms involving frequent task-switching, like the Wisconsin Card Sorting Task [93] or the number-color manipulation introduced in [73], lead to fatigue and behavioral aversion. As above, performance on each of these tasks has been shown to be sensitive to incentives [73, 94].

Measurable hallmarks of mental effort Mental effort often evokes a feeling of subjective displeasure, negative emotion, or a desire to quit. Measuring this negative affect can be accomplished in multiple ways. The most direct method is to elicit direct subject reports of feelings such as frustration, anxiety, unpleasantness, or the desire to avoid the task in the future [71, 70]. The potential for bias implicit in the elicitation of self-report [95] has led researchers to rely instead on implicit measures of subjective experience, such as the affective priming paradigm [96, 97]. In this paradigm, priming subjects with stimuli inducing positive or negative emotions reliably affects response time latency when responding to affect-categorized probe words.

In addition to a self-report of displeasure, people can exhibit a dislike of cognitively demanding tasks by simply avoiding them. "Demand-selection tasks" are a widely-used experimental paradigm designed to measure subject avoidance of cognitively demanding tasks [98]. A typical experimental design is to create several versions of a task with a hidden or explicit difficulty parameter (such as the 'N' in the N-back task, or a task switching rate). Subjects are free to choose from among the task options. In some

experiments, no financial incentive is tied to task engagement and subjects' engagement choices are taken to reveal a bias against the less frequently chosen tasks or task parameters [73]. In others, subjects are offered the option of choosing between task options, in which each is assigned an explicit monetary reward. By varying reward magnitudes and observing subject choices, relative preferences among task difficulties can be measured quantitatively [94, 65]. Using incentives to induce subjects to engage in mentally effortful activities is particularly appealing, as it affords the application of frameworks from behavioral economics, including quantification of effort in terms of a currency, and explicitly framing mental effort as a cost to be weighed against the benefits of a reward. Preferences for effort avoidance can also be revealed by subject behavior within a given task. For example, Droll found that rather than using working memory to capacity in a demanding task, eye movements indicated that subjects only sampled stimulus information as-needed [85].

Sustained mental effort also leads to cognitive fatigue, characterized by a feeling of increased effort [99], increased reaction times, decreased accuracy [75], weariness and boredom (see [100, 101], cited in [12]). One way to measure the degree of fatigue induced by a particular task is by using the so-called 'dual-task paradigm', in which subjects are asked to perform two different tasks in sequence. The cognitive difficulty of the first task is varied across subjects, and relative performance on the second task is compared across conditions (see [99] for a review). A performance decrease in the second task is taken to indicate a 'depleting' effect from the first task, though exactly what is depleted is a matter of much debate, and the size of the effect is often small [102].

Finally, engagement with mentally effortful tasks produces measurable biophysical changes often associated with stress, including increased heart rate, increased blood pressure, and change in skin conductance [103]. Unlike behavioral measures, these changes are often autonomic and readily replicable. However, care must be taken not to conflate the cause of such changes with other potential sources of stress, such as time constraints or the commission of errors.

What are the popular theories explaining mental effort? There is general agreement that the aversive phenomenological experience of mental effort serves to negatively influence an individual's decision to engage or persevere in a task. The

feeling of mental effort is a demotivator, a behavioral feedback mechanism provided by evolution. This phenomenon parallels physical effort, which has the same subjective structure and impact on demotivating behavior. While physical effort corresponds to muscle utilization and is empirically observable via increased oxygen uptake, increased heart rate, and an increasing concentration of metabolic byproducts in cells [104, 105], mental effort is typically assumed to be a quasi-phenomenon that reflects a sort of calculus in which cognitive load is traded for extrinsic or intrinsic benefits [60]. As such, mental effort is treated as an abstract cost in a cost-benefit analysis, though there is some disagreement about the nature of the cost.

This disagreement results from various attempts to map effort-related costs to key variables in decision making frameworks, typically borrowed from economics or control theory. For example, Kool and Botvinick suggest that mental effort is a temporal labor cost to be weighed against cognitive leisure [10]. In a similar spirit, Kurzban et al. have proposed that mental effort from task engagement reflects an opportunity cost from not engaging in other tasks [12]. Other models suggest that rewards expected from engaging in cognitive control are judiciously weighed against the intrinsic costs of the required effort [11]. Perhaps mental effort simply discourages use of limited-capacity shared resources like working memory and information transfer ([106] echoes earlier ideas of a 'multiple resources' [107, 108] with limited capacity [109]). Because these costs are associated with generic variables in decision models in each case, these accounts do not provide a normative explanation for why some tasks, and not others, evoke effort.

How do metabolic factors relate to mental effort? Despite the analogy with physical effort, there is little evidence that mental effort is related to the use or limited availability of metabolic resources, and suggestions to that end have been met with skepticism [110]. If mental effort indeed reflects metabolic resource utilization, we would expect a two-way causal connection between mental effort and resource availability: effort should deplete the resource, and a depleted resource should make engaging in effortful tasks more difficult. Regarding the first of these, there is little direct evidence to suggest that blood glucose, the most obvious metabolic resource, is meaningfully depleted following mental effort. While there is some evidence that sustained mental effort results in a measurable decrease in blood glucose levels [111], the decrease (typically $<$

1 mmol/L) is not nearly enough to account for the level of fatigue typically experienced following decreases of over 10 mmol/L [112].

The most thorough investigations of the relationship between cognitive function and resource depletion involve the study of the so-called 'ego-depletion' effect, in which subjects in a dual-task paradigm perform worse on the second task if the first task is particularly demanding [113], implying that the first task has 'used up' some underlying resource, presumably energy. Upon extensive replication this effect was found to be small or nonexistent [102]. Several studies claimed that imbibing a glucose drink after the first task improved performance on the second task [114], but again the causal mechanism has more recently been called into question [115].

In the other direction of the causal chain, evidence of a clear relationship between resource availability and performance of mentally effortful tasks is abundant. Lowering of blood glucose via an insulin drip or fasting has been shown to impair working memory [116], declarative memory [117], attention [118], the speed of decision-making [119], and performance on the Stroop task [120] and Go/No-Go task [121]. Working memory is particularly sensitive to glucose levels, with observable impairments occurring even with moderately low glucose levels still within the normal range [116, 122]. Moreover, memory performance can be improved with moderately higher blood glucose levels of 160 mg/dL in both animals [123] and humans [124]. Motor tasks such as the finger tapping task, on the other hand, are not sensitive to moderate manipulations in blood glucose [121, 125, 126]. In general, it appears that mentally effortful tasks are more sensitive to blood glucose levels than non-effortful tasks. For a thorough review see [112]. While these findings do not constitute evidence that the mentally effortful tasks use more energy than other tasks, they do suggest a strong dependency between the availability of metabolic resources and successful engagement in effortful tasks.

5.3 What's missing

The core challenge in modeling mental effort is providing an integrative account of the various scenarios in which the hallmarks of effort arise. A similar collection of effort-related phenomena (fatigue, avoidance, sensitivity to incentivization, and negative affect) are observed from engagement in seemingly unrelated types of tasks, strongly

suggesting a single underlying mechanism of effort. While variables like *control* [11] and *throughput* co-vary with effort for some categories of tasks, these explanations are hard to apply to the effort experienced from engagement in novel tasks. Furthermore, introducing intermediate 'cost' variables not grounded in biological constraints begs the question: *why* are control and throughput costly?

We believe that these gaps can be filled in a simple and unified manner by adopting the hypothesis that mental effort reflects the energetic costs of task-related information representation and transmission in the brain. In what follows, we identify three problems in the contemporary literature on mental effort, and suggest that identifying mental effort as a proxy for energetic information representation costs provides a unified and parsimonious solution to each. In the remainder of the paper, we provide theoretical and simulation-supported evidence for the claims made in this section.

Gap 1: allocation across tasks rather than within tasks

The influential models of mental effort mentioned in Section 5.2.1 ask how the brain allocates cognitive resources over time, and provide candidate algorithms for doing so in a way that maximizes reward and minimizes effort via task selection. However, there is abundant evidence that we minimize mental effort *within* tasks as well, sometimes using "fast and frugal" heuristics [66] to follow a "law of least mental effort" [67] rather than engaging in "intrinsically costly" effortful cognitive processes [10]. We feel that a full account of mental effort should be able to explain how effort is minimized within a task, and indeed what "resource" is minimized along with mental effort.

Solution 1: mental effort tracks information transmission and representation costs

In the spirit of David Marr's computational level of analysis [7], the phenomena of mental effort minimization while performing tasks may be viewed as a solution to a particular problem the brain is trying to solve: maximizing reward over time while minimizing resource utilization. When viewed across tasks, solutions to this involve comparing task demands and benefits, and result in selective engagement with tasks. This is the scenario addressed by most models of mental effort, described above. Even *within* a given task, however, there is the opportunity for optimizing the efficiency of encoding, representing,

and transmitting the task-related information required to perform the task successfully. The suggestion that the brain develops mechanisms for efficiently encoding information about the natural environment is an old and well-tested idea called the Efficient Coding Hypothesis [33]. Though the evidence for the Efficient Coding Hypothesis has primarily been sought at the level of sensory systems, the possibility of its application at the level of cognition and task learning offers a fruitful and normative approach for the investigation of mental effort and learning. In cases where errors are not costly, subjects may prefer to maintain low-fidelity representations of task variables, an option easily incorporated into a signal-transmission model of mental effort, which may also manifest as cognitive biases.

Taking the perspective that mental effort tracks information transmission and representation costs allows us to predict that as the brain learns to efficiently encode task-related information, costs of information transmission should decrease, and the feeling of mental effort should decrease. The tools of information theory describe bounds on signal efficiency as a function of task statistics 'in the world' and their relationship to the statistics maintained by the encoder and decoder. As stated above, this allows us to predict both mental effort decrease and response time decrease as a function of task practice.

Gap 2: unified explanation of phenomena

Mental effort is produced by utilization of the seemingly distinct mechanisms of working memory and attention use, 'conflict' override and control, engagement in novel tasks, and task-switching. Each of these conditions has been shown to produce the subjective feelings associated with mental effort, namely fatigue, responsiveness to incentives, a desire to quit, and negative affect. As this cluster of phenomena appear in tandem with each other, they may share a common underlying cause despite the apparently distinct scenarios in which they arise. This has been acknowledged to some degree in the literature on 'cognitive control'; however, 'control' is typically used as a synonym for 'allocation of effort' [59, 11], providing no explanatory power as to why these processes (and not others like simple object recognition, habitual responses, or simple motor movements) are effortful or require cognitive control.

Solution 2: mental effort tracks information transmission and representation costs

As we show below, transmission costs can be represented as a function of both throughput and encoding efficiency. We would therefore expect high costs in cases where throughput is high (demands on working memory and attention) or efficiency is low (novel tasks, conflicting tasks). We suggest that task switching falls into this latter camp, and results in effort when an encoding for one task is used to perform another task. Information transmission costs thus provide a unifying explanation that predicts the scenarios in which we expect mental effort to arise, incorporating throughput, learning, conflict, and task switching.

Gap 3: characterizing rather than explaining mental effort

A full account of mental effort should include a normative explanation for the conditions in which it arises. Contemporary accounts of mental effort [91, 11, 127, 106, 128] provide characterizations of the allocation of mental effort and cognitive control. Mental effort and cognitive control are treated as 'intrinsically' or 'inherently' costly, but it is not clear why some processes, and not others, should incur a cost. Authors certainly acknowledge that the level of mental effort experienced has some relation to task demands. For example, it is commonly accepted that the effort induced by the N-back task scales with N [65], and that task switching costs are a function of switching frequency [73]. But no useful explanation is provided as to *why* more frequent switching or a higher N produces a greater degree of mental effort. When explanations are given in other literature, effort is explained to be the result of "resource utilization", "cognitive load", or "task set loading" costs, but no account is provided sufficient to produce predictions of mental effort magnitude [91]. The case is similar with cognitive control tasks like the Stroop task. It is assumed (and is borne out by evidence) that such tasks are subjectively costly. Explanations of the source of cost involve the "override of pre-potent responses", but again there is no normative explanation for why such override *should* be effortful.

The suggestion that mental effort reflects opportunity costs [12] represents a significant exception to this pattern. In this view, effort reflects a relative value judgment: a task feels effortful if cognitive capacity can be better utilized elsewhere. Effort is a signal

indicating the sub-optimal allocation of cognitive resources. This model explains the conditions under which effort arises, and attempts to account for the existence of mental effort in addition to the algorithm of its allocation. Despite this, the model of effort as opportunity costs fails to explain, in a normative way, which tasks should produce the strongest sensations of effort, or the manner in which task parameters influence the feeling of effort.

Solution 3: mental effort tracks information transmission and representation costs

In order to perform a task, a subject chooses actions in response to stimuli. Assume that the subject has been instructed in the task paradigm and the 'correct' action in each scenario is known, as is the case in nearly every task designed to induce mental effort. We can consider the stimulus to be a message transmitted from the sense organs through the brain to an action-selection mechanism. As described in Chapter 2, the quantity of information transmitted to the neural action-selection mechanism is defined by a signal receiver's uncertainty about which stimulus might be present, which in turn is a function of the probability distribution of task stimuli. In this way, the magnitude of information transmission, and thus transmission costs, can be described (in part) as a function of task properties. To the extent that mental effort tracks information transmission costs, this affords a normative account of which tasks *should* be experienced as costly: tasks with higher receiver/decoder uncertainty (e.g. high working memory load), or with a higher required response rate (e.g. vigilance tasks), or with an inefficient code (e.g. novel tasks).

As we describe below, transmission costs must incorporate the task properties as *assumed* by the receiver, a fact that may explain reduction of mental effort with task practice. Where experience with the task affords subjects a better model of task statistics, transmission costs, and therefore effort, should decrease.

Our approach agrees with existing accounts in that we acknowledge the demotivating role played by the phenomenological experience of mental effort, and we do not deny that the decision to engage in effortful tasks is a function of incentives. In quantifying the cause of mental effort in terms of task demands and subject learning, we contribute a normative explanation of the source of effort.

5.3.1 Summary & approach

The goal of this chapter is to argue for the plausibility and parsimony of an information-theoretic interpretation of mental effort as a function of the energetic costs of information representation and transmission. To instantiate this investigation, we use the Bayes-Poisson model introduced in Chapter 2. The model consists of an array of Poisson processes used to encode and transmit information, and a Bayesian observer and decoder to receive information. We utilize this model for two reasons. First, we wish to demonstrate how the theoretical constraints we consider are reflected in a working model of information transmission. Second, we tie mental effort to an above-baseline spike rate, providing a high-level model that provides hypotheses for an implementation-level investigation of mental effort. However, we emphasize that throughout the remainder of the text, we are not proposing *implementations* of efficient information transmission in the brain. We remain largely at Marr's first level of analysis and ask, if the brain were attempting to represent task-related information efficiently, what behavioral characteristics might result? We engage in analysis at Marr's second level by utilizing a model of a rate code, but do so primarily to demonstrate the validity of our first-level analysis, and to instantiate a code in which we can measure energy use. We hope that this approach, which makes qualitative (and some quantitative) predictions, convinces the reader that by assuming a driving process of efficient information transmission *somewhere* between the sense organs and resulting actions, we gain some clarity and parsimony in understanding the phenomena associated with mental effort.

The remainder of the text is divided into three sections. In Section 5.4, we introduce the reader to the relevant technical details of information theory, signal power, and energy utilization. In doing so, we emphasize features that have qualitative parallels in the behavioral psychology literature. We also briefly summarise the Bayes-Poisson model described in Chapter 2. In Section 5.5, we enumerate the behavioral and neural phenomena we would expect if mental effort in fact tracks transmission costs, and survey the experimental results for each. For several of these phenomena, we provide a working implementation using the Bayes-Poisson code that provides a qualitative, functioning example of the principle in question. The goal of this section is to convince the reader of the plausibility and parsimony of the information-theoretic explanation of mental effort. In the final section, we discuss implications of the proposed models and highlight

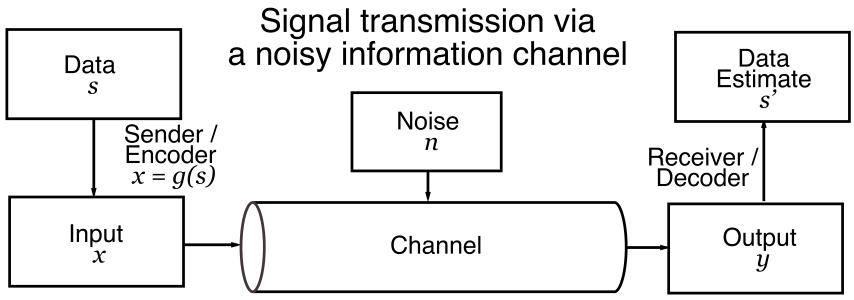


Figure 5.1: Channel model of information transmission. Adapted from [19], with permission, and inspired by Shannon's original diagram in [13].

remaining areas of uncertainty.

5.4 Energy, information, and time

In this section we provide a brief introduction to the relevant information-theoretic concepts that we use in the remainder of the chapter. As formalized by Claude Shannon, information transmission involves communication between a sender and a receiver (see Figure 5.1). The receiver knows that some message will be sent, and has uncertainty about the content of the message. The uncertainty is called 'Shannon entropy' or just 'entropy' and denoted H. Entropy can be quantified in *bits*, in which case it represents the expected number of binary yes/no questions it would take to uniquely specify the message sent. The sender transmits a message over a noisy medium, such as wires, sound waves, or neurons, possibly coded so as to maximize the information transmission rate over that medium. Information has been transferred from sender to receiver to exactly the extent that the receiver's entropy has been reduced.

We constrain our investigation to message transmissions in which a message is taken from a finite *alphabet* and *encoded* through use of a *codebook*. In practice, this means that a discrete message is converted into current perturbations, or pulses of light, or neural spikes; our implementation is described in Section 5.5.

Messages are transmitted from the source with some relative frequency, described by a probability distribution P. The receiver maintains a *guess* as to the message frequency represented by a probability distribution Q. If $Q \neq P$, messages are generally longer

than necessary (this is also true for source-coding, see [20] for in-depth discussion). As discussed in Chapter 3, the expected extra message length is defined by the Kullback-Leibler divergence between P and Q, denoted $D_{KL}(P(X)||Q(X))$. In scenarios in which the encoder is encoding messages by relying on an inaccurate model of the distribution of the source, the message length will be longer than necessary. We return to this point in Section 5.6.3, where we discuss the energetic costs of engaging in novel tasks.

5.4.1 Energy costs and mental effort

In a physical communication, a signal takes the form of some perturbation of a medium, such as the electromagnetic field, the air, or the cross-membrane voltage of a neuron. Perturbing the medium takes energy. The amount of energy used to affect this perturbation is referred to as the signal's *power*. From basic physics we know that energy quantifies the total power expended over time, where P_t represents power at time t:

$$E = \int_0^T P_t dt$$

If signal power is constant, we can simplify the expression to:

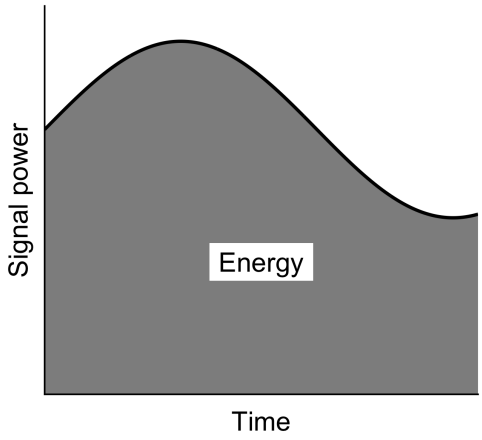
$$\text{Energy Used} = \text{Power} \times \text{Time}$$

Signal power, integrated over time, describes the energy used in signal transmission. With the cursory discussion of the relationship between signal power, information transmission rate, and energy utilization in hand, we offer the following analogy to the phenomena of mental effort:

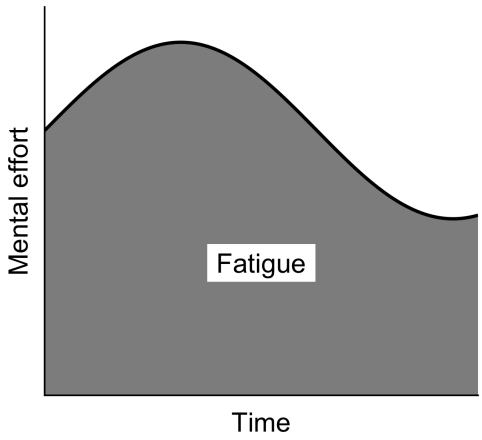
$$\text{Energy Used} = \text{Power} \times \text{Time} \tag{5.1}$$

$$\text{Fatigue} = \text{Mental effort} \times \text{Time} \tag{5.2}$$

We propose that this is more than just an analogy: we suggest mental effort is a phenomenon that tracks instantaneous energy utilization in the service of tasks. However, this simple model alone does not explain why, for example, energy utilization in service of cognitively demanding tasks is effortful, while largely equivalent energy utilization



(a) The total energy used when transmitting a signal is the sum of instantaneous signal power.



(b) Fatigue is hypothesized to reflect accumulated mental energy utilization (though only above a baseline rate, see also Figure 5.3).

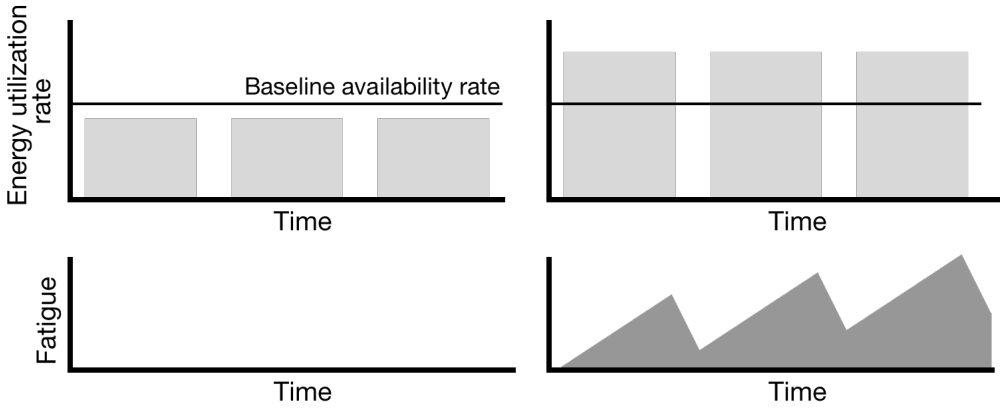


Figure 5.3: Accumulation of fatigue. Fatigue is hypothesized to accumulate when the spatially local rate of energy utilization exceeds a baseline rate of energy availability provided by an outside source, e.g. blood glucose.

in the visual cortex does not give rise to the same experience of effort. We propose that the difference lies primarily in the *variability* of energy utilization. In brain regions for which energy utilization rate is constant, the inflow of energy in the form of blood glucose is a sufficient source of energy. For regions with task-related variability in activation, it is conceivable that energy utilization rate occasionally exceeds the baseline input rate (see Figure 5.3 for a schematic). In these cases, the brain region would need to utilize an alternative source of energy such as astrocytic glycogen, which is a limited resource. This proposal is currently an untested hypothesis, but it is plausible, and we discuss experimental evidence related to glycogen utilization in Chapter 6. For the purpose of this chapter, we simply suggest that dismissing the energy-effort connection out of hand is unwarranted.

Nevertheless, we do know that sustained mental effort results in cognitive fatigue. Behavioral evidence suggests that cognitive fatigue correlates with the inability to sustain mental effort (and signal power), and leads to effects characteristic of sending signals with lower power: slower response times and higher error rates. The remainder of the chapter is dedicated to elaborating on these claims by instantiating them in simulation results using a simple rate-coding model of neural firing, and then surveying related findings in behavioral psychology.

5.5 A variable-length code

In this chapter we make the general claim that mental effort tracks signal transmission costs, and specifically the *energetic costs* of transmitting information. In service of the plausibility of this argument, we briefly review the Bayes-Poisson code introduced in Chapter 2. The coding mechanism can be interpreted as a simple algorithm-level model of a neural rate code which can be used to transmit variable-length messages. We use this code to establish the neural plausibility of the proposals throughout this chapter and to ground the theoretical considerations in a worked example. An important property of the coding scheme which we did not emphasize in Chapter 2 is that coding costs can be measured in 'spikes', where each spike costs a fixed amount of energy. Because of this, the costs of task-related information transmission can be directly measured, and the relationship between information throughput, task novelty, and energy costs can be

directly quantified.

Recall that in the Bayes-Poisson model, messages to be communicated are taken from an alphabet of discrete symbols A_s. The encoder consists of an array of Poisson processes, each producing points or 'spikes' independently at a given *noise rate* λ_N. In the basic model, the number of Poisson processes equals the number of symbols in the alphabet, namely m. The codebook maps each symbol to a configuration of rates. For simplicity, we use a '1-hot' encoding, such that there is a correspondence of Poisson processes to symbols. When a given symbol is transmitted, the rate of its corresponding Poisson process is increased by a *signal rate* λ_S, to a total rate of $\lambda_N + \lambda_S$.

The receiver observes the sequence of spikes emitting from each Poisson process and uses Bayesian inference with a prior distribution Q to infer which process is firing at the higher $\lambda_N + \lambda_S$ rate, and thus which symbol is being transmitted. We assume, again for simplicity, that the receiver knows the values of both λ_N and λ_S.

The receiver begins each transmission at time $t = 0$ with an initial uncertainty $H(X)$ regarding the symbol being transmitted, reflecting its prior distribution $P(X)$ of the possible codewords. As time passes and observations $Y = y$ accumulate, the receiver accumulates information regarding which transmission is most likely and uses Bayes' Rule to update the prior and obtain a posterior distribution $P(X|Y = y)$ over messages. The entropy of that distribution is calculated, as illustrated in Figure 2.3. When the receiver's entropy reaches a pre-defined threshold, the receiver stops observing. We interpret the time between the beginning of observation and the observation stopping time as the transmission time, or the response time.

In several of the sections below, we use this coding scheme to model the transmission of task-relevant variables. In each case, we show that extra extra energy is required in exactly the task circumstances that give rise to the feeling of mental effort.

5.6 Why some tasks are more difficult than others

In this section, we review the categories of tasks that induce a feeling of mental effort, and describe how the demands in those tasks are related to their inherent information transmission costs, in terms of average spike rate.

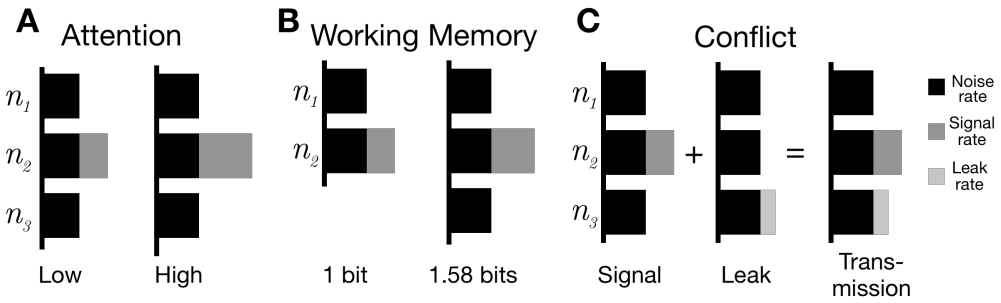


Figure 5.4: Allocating more signal power improves performance in tasks requiring attention, working memory, and response conflict. (A) Higher signal power λ_S leads to faster response times at the cost of greater energy use. (B) More power must be allocated to transmit more information in the same amount of time. (C) In conflict-inducing tasks, signal power must be allocated to overcome a 'leak' signal induced by distractor stimuli.

5.6.1 Attention

Attention is the term given to the process of accepting the deluge of raw input from the ears, eyes, and other sensory organs, and selecting which parts should be made available to executive processes, and which should be filtered out [129]. Humans and other animals have some ability to 'endogenously' direct our attention in a 'top-down' fashion, making task-relevant information available to processes of executive control while filtering irrelevant 'noise' [130]. Subjects are said to 'allocate attention' to a particular set of environmental features. Attention is so closely associated with cognitive effort that the two have been sometimes seen as identical [131]. In addition to the target of attention, the *degree* of attention can be modulated at-will, often in response to motivational incentives [131]. By increasing so-called 'attentional gain', subjects can respond to stimuli more quickly and with higher accuracy. In this section, we show how the Bayes-Poisson framework models attentional gain, and suggest that mental effort corresponds to signal power, or more explicitly, energy use per unit time. The model thus provides a mechanism for quantifying the energetic costs associated with attentional gain.

Tasks requiring a high level of attention for a prolonged period are known as 'vigilance tasks'. In these tasks, subjects must monitor stimuli for infrequent changes that may be difficult to perceive. Sustained engagement with such tasks requires 'hard mental work' [82]. Sustained attention also leads to an accumulating feeling of mental fatigue

and a decrease in performance over time [132]. Vigilant attention is associated with a notable change in skin conductance response [133]. Intensive endogenous attention is strongly correlated with the hallmarks of mental effort, and using it acts as a cost [134].

While some degree of attention is necessary to recognize stimuli and respond where appropriate, deploying a higher degree of attention can reduce error rates [135] and speed subject response times [136] in certain tasks.

The prevalent view of the neural implementation of attention suggests that the deployment of attention increases neural firing rates in response to the 'preferred' features of the stimulus, or the features to which the individual is attending [130, 137], thereby increasing the signal-to-noise ratio of neurons responding to behaviorally relevant stimuli over a background rate. Recent work suggests that increased neural gain may serve to increase the performance of behavioral response rather than improve the neural representation of attended stimuli per se; this is particularly noticeable in situations with visually similar but differently relevant stimuli [138]. This perspective supports recent theoretical suggestions that neural coding of environmental stimuli may involve an optimization for behavioral or energetic efficiency rather than maximize mutual information with the environment [25], as assumed by the Efficient Coding Hypothesis [33].

We instantiate controllable attentional gain in our Bayes-Poisson model by changing the signal rate λ_S allocated to the neuron 'tuned' to the presented stimulus, similar in nature to neural gain models of attention, thereby increasing the ratio of the signal rate λ_S to the noise rate λ_N (see Figure 5.5). The signal power λ_S represents spikes per second, which translates directly to energy use per second. We model the variation in attentional throughput by fixing a set of messages to transmit and varying allocated signal power.

We model varying rates of 'vigilance' as energetic resources allocated to signal transmissions (though it may alternatively be captured as forced noise suppression, see e.g. [24]). To capture the effect of changing signal power on information throughput, we simulated 1,000 transmissions at varying signal powers for each of three entropy thresholds. For each transmission, we calculated the information transmitted by computing the Kullback-Leibler divergence between the receiver prior and the receiver's posterior at decision time (see Chapters 2 and 2 for a more thorough discussion of this procedure). Information throughput is computed as the information transmitted divided by

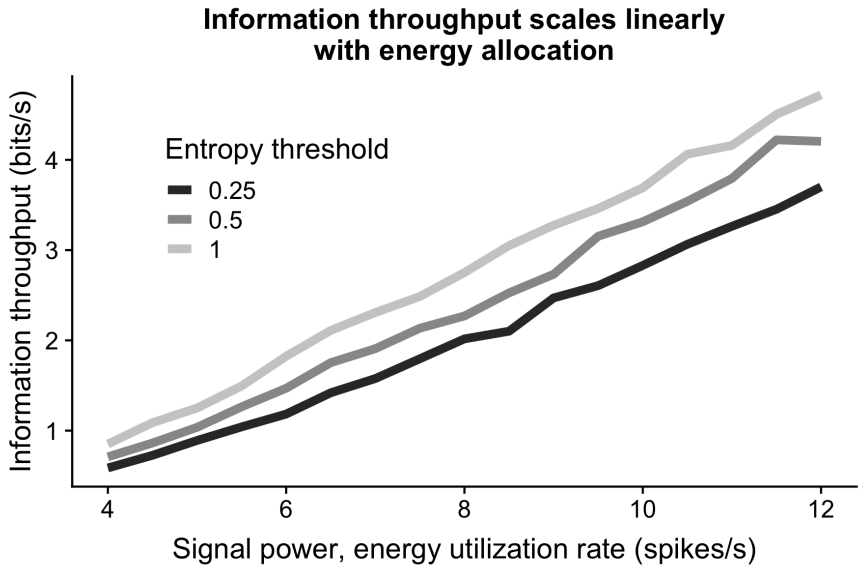


Figure 5.5: Increasing signal power λ_S increases the rate of information transmission. Information transmission rate was calculated by computing the transmitted information as the KL-divergence of the receiver prior and the posterior at stop time, as described in Chapter 2, and dividing by the total time taken for the transmission. Simulations were performed with a noise rate λ_N of 10 spikes/s, and an entropy threshold of 0.5 bits, with 4 possible messages and an initial receiver entropy of 2 bits. Entropy decreases most quickly at start of the transmission and decays exponentially (see Figure 2.3 in Chapter 2), so transmission rate is higher, on average, with a higher entropy threshold.

the transmission time. As can be seen in Figure 5.5, throughput increases linearly with allocated signal power. We suggest that this is a reasonable high-level model for the relationship between mental effort (as indexed by signal power) and response time in attention tasks, analogous to the way drift rate is associated with evidence accumulation rate in the drift-diffusion model [22]. As discussed in Chapter 2, increasing signal power also shortens average response times and decreases response time variance (see Figure 2.5).

5.6.2 Working memory

As with endogeneous attention, working memory is a cognitive resource whose extensive use induces a feeling of mental effort. The term 'working memory' refers to the maintenance of the value of task-relevant variables in a manner such that they can be quickly retrieved and used to perform action selection [81]. Working memory is famously capacity-limited, but the nature of the capacity is still a matter of debate. While early theorists modeled memory capacity as a set of discrete slots [31], recent research supports models of memory as a variously allocated continuous resource [139]. Despite growing acceptance of a continuous resource model of working memory, the nature of the resource remains unclear. We suggest that the limited resource may be an energetic resource, specifically the rate of available energy that can be allocated to maintaining a particular signal with a low rate of error.

Some minimum maintenance of task-relevant variables is required to perform almost any ecologically valid task, but extensive utilization of working memory is effortful and aversive. Subjects seem to minimize demand for working memory use when possible, leaving readily available information 'in the environment' to be accessed as needed rather than incorporating it into a memory representation [85]. Subjects self-report a desire to quit following tasks with a high working memory load, with larger memory demands leading to a higher urge to quit [74]. Westbrook et al. devised a demand-selection task in which subjects could choose to perform the N-back task with a high or low value of N [65]. They found that subjects required a larger financial incentive to select a higher value for N, thus preferring lower values of N for a given reward. These examples are emblematic of a larger body of findings indicating that performance on working memory tasks is sensitive to incentives [140, 141], which conversely suggests that subjects would

rather not utilize a high level of working memory unless the intrinsic cost is offset by some reward.

While a useful and full-featured model of working memory is beyond the scope of this chapter, we suggest that working memory can be treated as the transmission of information from one point in time to another point in time. This recurrent-style memory model is similar to the the rehearsal model of working memory [142]. Working memory costs can be conceptualized as transmission costs, and capacity can be modeled as the maximum rate of transmission given signal power constraints. If, as we suggest, effortful working memory implies the possibility of variable resource allocation in the presence of incentives, we could model changes in working memory capacity as a transmission rate influenced by allocated signal power.

Behavioral findings suggest that both attention and working memory are subject to controllable, variable use. Intensive use - either in terms of high attentional gain or high working memory capacity with low error rate - is subjectively effortful, behaviorally aversive, and results in eventual fatigue. We have presented a model that parsimoniously describes these phenomena in terms of allocated signal power. Signal power must be paid for with energy, a fact that immediately grounds our proposal in terms of available energetic resources. If signal power is identified with neural gain, as seems reasonable [143], the rate of available energy (in the brain, via blood glucose or astrocytic glycogen reserves) becomes both a cost and a limitation. Incentives could induce a temporary boost in signal power, but only to the extent that surplus energy is available (see Chapter 6 for further discussion).

5.6.3 Novel tasks

To observe that novel tasks are often difficult and error-prone is mundane; indeed, much of psychological research considers this an axiom, an established truth from which we can investigate properties of learning. Nevertheless, the pervasiveness of this phenomenon and its presence on the list of task circumstances that induces mental effort requires that it be included in any account that purports to explain mental effort. In this section, we show that familiarity with a task can be modeled as an estimate of the probability distribution of stimuli whose contents must be encoded and transmitted from a sender to a receiver. As familiarity increases through practice, receiver expectations about

stimulus probabilities become refined, making it possible to decode the same signal with a shorter transmission.

Despite rarely being considered in the cognitive control literature, engagement with novel tasks has the hallmarks of deployed control: engaged and focused attention, utilization of working memory, a conscious awareness of the task goals, and deliberative direction of behavior [144]. Engagement in novel tasks is experienced as effortful, as anyone can attest who has learned to play an instrument or speak a new language. As the task is practiced, however, it becomes progressively easier, often to the point of being executed effortlessly or even habitually or automatically [26, 29]. Given that performance of even relatively simple new tasks requires engagement of cognitive control, an apparently expensive and constrained resource, some suggest that the complex set of behaviors that characterize daily life is - and must be - largely composed of 'automatic response patterns' [145]. Tasks once difficult are practiced until they become effortless; once effortless, they can be performed quickly, effortlessly, and in parallel [78]; perhaps all expertise is simply the result of practice [146].

We propose that novel tasks are costly, from the perspective of transmitting a signal, because the transmission system is not optimized for the task in question. In variable-length codes like the Hamming code and the Bayes-Poisson code, code length is a function of the assumed probability distribution Q of the stimulus in question, that is, of the messages to be transmitted. In a well-designed code, Q will be similar to the actual source probability distribution of messages P. When beginning a new task, a subject has no way of knowing P - yet must transmit task-related messages all the same. How might this be possible? To answer this question, we can borrow the concept of 'universal' coding [20] from information theory.

A universal code is one which, while not optimized for any particular message distribution, should perform adequately for any *expected* distribution. Universal coding can be thought of as the solution to a 'game in which the coder chooses a code that attempts to minimize the average length of the representation and nature chooses a distribution on the source sequence' (see [20], p. 428). This is analogous to the situation a person finds themselves in when beginning a new task: they are perhaps familiar with the visual and auditory statistics of the environment, but they do not yet know which environmental features are relevant to the task, or the frequency distribution describing

those relevant features.

We can model this scenario with the Bayes-Poisson model by beginning a task with a very large alphabet and a uniform Q distribution over transmitted signals. The large alphabet reflects the idea that a subject can be able to recognize a high number of stimulus configurations, each mapped to a symbol in the alphabet, and could potentially encode and act on each if required by the task. However, the uniform distribution Q over possible symbols represents a 'universal' code, and indicates that the subject is not sure which stimuli will be relevant to the new task, or at what frequency.

It may seem counter-intuitive to suggest that subjects include stimulus configurations in their alphabet that task instructions do not explicitly enumerate as important to the task as hand. However, behavioral evidence reliably demonstrates that task novices are more likely to notice and encode task-irrelevant stimuli than experts at the same task. In a 2013 study of inattentional blindness [147], Drew et al. inserted a picture of a gorilla in radiology images, in reference to the now-classic study by Simons and Chabris [148]. Despite often looking directly at the location of the gorilla, experts typically were not aware of the its presence. Experts presumably have a very-well-developed Q distribution, which includes near-zero probability mass for stimulus configurations that include gorillas, effectively eliminating the chance that any gorilla-related message would be accurately transmitted. Novices, on the other hand, visually encoded and thus were able to notice the contextually inappropriate feature of the stimulus.

Figure 5.6 gives the average cost of signal transmission, in terms of time, and thus spikes and energy, as a function of the difference between Q and P. Unfamiliar tasks – tasks for which the receiver does not have an accurate prior distribution over message transmission frequency – are more costly on a message-by-message, and thus trial-by-trial, basis.

Once again, claiming that task-related information transmission tracks mental effort allows us to make normative claims: novel tasks *should* be more effortful, because a task-optimized code, or in our case a task-optimized prior, has not yet been developed. The notion that the brain adapts neural rate codes to task statistics is a direct analogue to the Efficient Coding Hypothesis [33, 37], which suggests that neural coding has developed over a developmental and evolutionary timescale to efficiently represent stimulus information in the natural environment - and implicitly requires that the coding

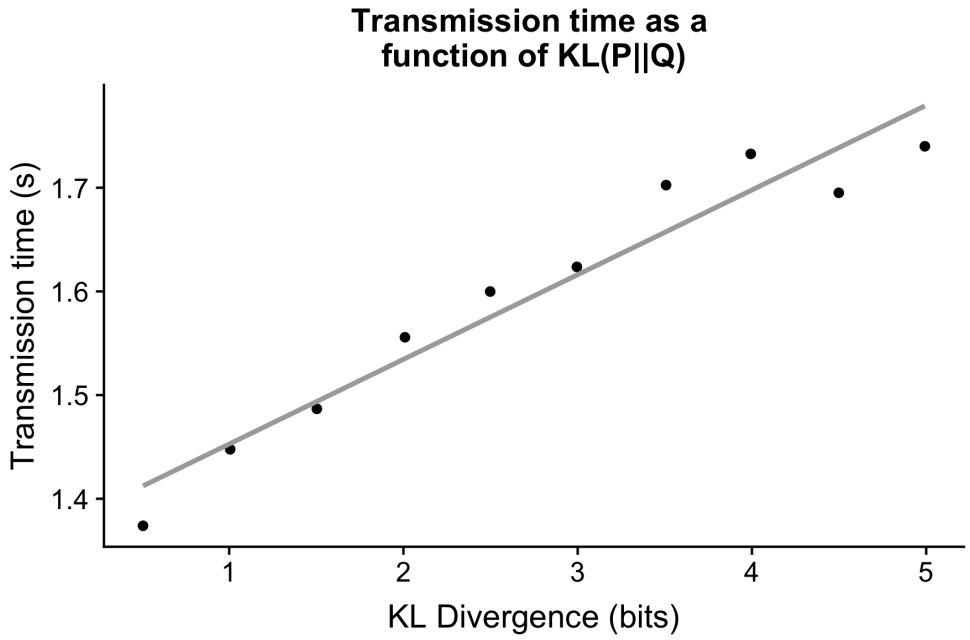


Figure 5.6: Average response time, and thus the amount of Poisson spikes and energy, increases roughly linearly with $D_{KL}(P||Q)$. Simulations were performed with a signal power $\lambda_S = 10$ spikes/s, noise power $\lambda_N = 10$ spikes/s, and an entropy threshold of 0.05 bits. A low entropy threshold is required to maintain relatively constant error rates across values for $D_{KL}(P||Q)$.

mechanism incorporates stimulus statistics from the natural environment. The Efficient Coding Hypothesis has been widely validated in early sensory systems [34, 35, 36]. We suggest that it also takes place at the scale of learning, in which signal efficiency is manifested as subject response times and a corresponding decrease in mental effort.

One interesting normative prediction of the development and use of task-specific codes, in the form of task-indexed Q distributions, is that acquired skill on individual tasks should not, as a general rule, transfer to other tasks. If our model of constructing task-tailored codes from a universal source code is appropriate, we would expect skills developed with over-practiced tasks to transfer less well than skills developed for moderately-practiced tasks. In general, if a task is understood as a context upon which a specific code is conditioned, or in which it is utilized, it is possible that practice effects might fail to transfer to a formally similar task without appropriate contextual cues [149].

5.6.4 Conflict

Some tasks evoke a tendency to produce responses that are not in accordance with the task instructions. For example, in the 'incongruent' condition of the famous Stroop task, subjects are asked to observe a color word, such as 'GREEN', drawn with a differently colored ink (e.g. red), and report the color of the text itself rather than reading the word [9]. When shown several words in sequence, subjects sometimes report semantic content of the word rather than its ink color. The Stroop task is said to induce a 'conflict' in responses: on the one hand, the task instructions say to read the word color. On the other, reading a word on a screen is habitual to the point of being involuntary: it drives a subject's 'default' response. In the typical framing, subjects who respond correctly to the task are said to 'override' a 'pre-potent response' or 'default action' [91]. The override is necessary because the 'habitual' response creates 'interference' with the stated task instructions. The deployment of habitual override is often called 'cognitive control', to highlight the contrast with automatic recognition-driven responses [59, 60, 91, 150, 106]. Cognitive control is colloquially said to 'bring more resources online' and 'reconfigure information processing away from default settings'. As with attention and working memory, possibly because it is a construct not entirely separable from those, cognitive control can be modulated. Increased control is demonstrated

after errors on conflict-inducing trials, in the form of increased accuracy and decreased response times (called the "Gratton Effect" [151]). The level of control is sensitive to motivational incentives for correct responses [59].

Deployment of cognitive control while performing the Stroop task and other conflict-inducing tasks such as the Stop-Signal task, Flanker task, or the Go/No-Go task induces symptoms characteristic of mental effort. Subjects find such tasks aversive [88, 73], frustrating [70], fatiguing, and show a desire to quit [74]. Conflicting trials, and especially errors on those trials, induce negative emotional affect [152, 69, 74].

The difficulty inherent in the Stroop task and other 'conflicting' tasks appears to arise from their eliciting multiple responses simultaneously. In the language of signal transmission we have been using, we might say that multiple signals are sent and *superimposed* in the incongruent and congruent conditions, whereas there is just one signal in the 'neutral' condition. The superimposed signals could be either complementary (as when the word and text color both indicate 'green') or contradictory (as when the word is 'red' but the color and desired response is 'green'). One of the signals - the one that corresponds to task demands, in this case naming the color of the text - is desirable. The other is habitual, a 'leaky' signal.

We model this leaky signal as shown in Figure 5.4C. The leak signal acts as a particular type of channel noise, which biases the receiver towards the signal it represents and slows the decrease of entropy. When the leak signal is congruent to the primary signal (as defined by the task instructions), simulated response times decrease compared to baseline. When the leak signal is incongruent to the primary signal, response times slow. Both of these phenomena qualitatively replicate the "Stroop Effect", matching behavioral results shown in humans [153]. For simulated trials spaced evenly in time, the incongruent condition requires roughly 33% more spikes to transmit the same messages as the neutral condition, and 65% more than the congruent condition. From these numbers, we would expect the incongruent condition to be more mentally effortful than the congruent condition. This is qualitatively consistent with reported effort and fatigue effects from participants engaged in the congruent and incongruent conditions of the Stroop, Flanker, and other conflicting-signal tasks.

We explore the phenomenon of cognitive conflict in greater detail in Chapter 4. We constructed a variation of the N-back task in which responses typically followed a regular

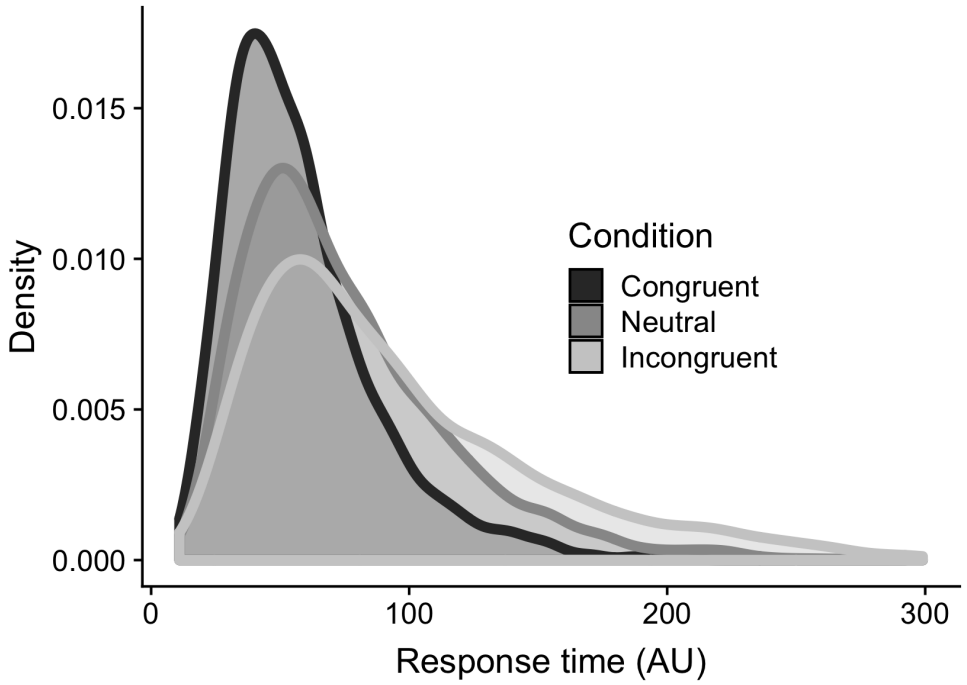


Figure 5.7: Reproduction of the Stroop effect. Signal transmission time is affected by the presence of super-imposed signals that are either congruent or incongruent with the primary, task-instructed signal. Figure 5.4C shows an example of an incongruent signal.

pattern. In doing so, we induced a habitual response that often predicted the same response as task instructions, but not always. In cases where the habitual response and instructed response conflicted, subject behavior showed hallmarks of conflict conditions on other cognitive control tasks: slower response times and higher error rates. In this case, however, it was not the stimulus itself that contained conflicting information, but rather a combination of stimulus information, information stored in working memory, and the prior expectation of a particular behavioral response. By incorporating the habitual response into the Bayes-Poisson model as a prior on *responses*, we are able to closely reproduce subject behavior with the model.

In the existing literature on response conflict and cognitive control, the existence of conflict is sometimes considered to carry an intrinsic cost [152]. We propose a subtle but important distinction between the energetic costs paid in service of task performance, and the 'meta-level' costs associated with conflict monitoring. Suppose that conflict-laden tasks are indeed more inherently effortful and costly to engage in at a high-performance level, as we argue above and as is supported by behavioral evidence. If so, such costs are arise directly as a result of task engagement. It is not the presence of conflict per se that is expensive, but rather the additional energy that must be expended (in the form of higher signal power or longer signal transmissions) that is costly. The observed avoidance of conflicting tasks might be better understood as the avoidance of the energy required to successfully perform the tasks, analogous to avoidance of tasks that demand a high attentional load or working memory capacity. In short, conflict is not special: it describes one of several task arrangements in which task success is only achieved by spending a high amount of spikes.

Task switching

Switching from engagement in one task to another slows responses and increases error rates in the time immediately following the switch [154]. Frequent task switching produces behavioral aversion [10, 73], subjective feelings of effort, eventual fatigue, and an overall decrease in performance [155], all of which are characteristic of mentally effortful tasks. But why should switching tasks be more effortful than engaging in each task separately? Performance decreases due to task switching are often explained by the need to load task-relevant information such as instructions and environmental variables into

working memory, or overriding the previously relevant stimulus-response associations.

We do not disagree with this view, though we feel that the high-level description of 'task-set reconfiguration' may explain the errors, but not the effort, that is associated with task switching. To understand why task switching might be subjectively effortful, recall that we have seen increased signal cost in two scenarios: (1) inappropriate prior distributions over symbols (as in novel tasks), and (2) superimposed signals from different attentional sets (as in conflict-inducing tasks). As we have shown, these both lead to additional cost-per-signal on average. They also lead to a higher error rate, with false-positives concentrated on outcomes with a high prior weight in the first case, and on 'conflicting' stimuli in the second.

We propose that in the case of frequent task switching, the 'task-set reconfiguration' can be understood as altering what to attend to, and updating the frequency distribution over the attended set. These correspond to the two mechanisms for error and slowdown we have seen above. If, when switching from one task to another, these two changes are not updated *instantaneously*, there will be a brief incompatibility between the mechanisms supporting signal transmission and the requirements and statistics of the task. As with novel tasks and conflicting tasks, we would expect this incompatibility to manifest as slower response times, higher error rates, and a higher signal-cost-per-message – in other words, a 'residual' switching cost, in both behavioral outcome *and* energy-use-per-signal. When seen from this perspective, the residual costs arising from task switching have the same structural source as those arising from a conflicting task or a novel task.

5.7 Discussion

A similar experience of mental effort arises in seemingly unrelated tasks that require extensive use of working memory or attention, novel tasks, tasks involving conflicts between possible responses, and paradigms involving frequent task switching. We have argued that in each of these cases, mental effort tracks signal transmission costs, and high performance in tasks requires energy use above-and-beyond that required by a baseline level of engagement. This perspective provides a principled connection between information-theoretic task requirements and perceived difficulty, filling a large gap in

the contemporary discussion on mental effort and cognitive control.

We propose that the Bayes-Poisson model described in Chapter 2 is a useful tool for modeling information transmission in tasks, as it provides an explicit representation of task cost in terms of transmission time and spike count. As we show in Chapter 4, the Bayes-Poisson model produces error rates and response time distributions that closely match human subjects in task conditions, while providing a theoretically principled way of understanding why these behavioral parameters shift as a function of task demands and structure. One goal of the current chapter is to encourage the use of the Bayes-Poisson model in understanding other tasks as well.

The deeper hypothesis we have endeavored to articulate is that the cognitive processes invoked in service of tasks can and should be measured in terms of energy utilization. Using the Bayes-Poisson model, we have argued for the *prima facie* plausibility that mental effort arises exactly when tasks require more energy, as measured by spikes, to successfully complete. While there is little doubt that hypoglycemia hampers cognitive function, any suggestion that cognitive operations utilize an operationally significant amount of energy is currently met with skepticism. We hope to alleviate some of this skepticism by demonstrating, via a simple model, a correspondence between spike counts and information-theoretic task demands. As spikes cost energy, this perspective unifies the computational and metabolic costs of task engagement.

The question of whether energy used in the service of tasks is of a large enough quantity to impact cognitive function is still open. However, as sustained mental effort leads to cognitive fatigue and a decrease in task performance that mimics the effects of hypoglycemia, there is a strong argument to be made that mental effort is a symptom of energy use above-and-beyond the rate of energy input from the blood stream. We have argued that information transmission in service of task completion is limited by available signal power, which corresponds to an available energy rate. However, we have also remarked that this appears to be a controllable resource: attentional gain, working memory capacity, and cognitive control in a conflicting task all appear to be capable of effortful temporary improvement. When modeled as an increase in allocated signal power, additional effort implies a temporarily higher rate of energy utilization. In addition to the blood stream, energetic resources are stored in a spatially localized distribution of astrocytic glycogen. As we discuss in Chapter 6, energy utilization whose

rate exceeds the availability of glucose from the blood stream utilizes this finite resource. It seems plausible that the phenomenological experience of mental effort reflects the tapping of this resource. While some experiments have found little regionally specific variation in energetic use as a function of task stimuli, these studies are primarily focused on sensory systems already relatively optimized to efficiently code the natural environment. We would expect task-related energy use increase and glycogen depletion associated with mental effort to instead occur in regions of the brain that can be flexibly reconfigured to meet task demands, such as the prefrontal cortex.

Our suggestion that information transfer in service of task completion is dependent on available signal power, and thus available energy, closely conforms to notions of bounded rationality originally articulated by Simon [156] and more recently by Griffiths [157]. A limited energy input rate driving signal power, even if temporarily boostable, bounds the fidelity of memory, the gain available to attention, and the degree over which cognitive control can be applied.

By instantiating mental effort as arising from the energetic costs of information transmission, we are able to cleanly distinguish between the often confused concepts of cognitive control and self-control. Cognitive control, in the form of attention or conflict-override, can be understood as energetic resources allocated to the task of information transmission. Self-control, in contrast, is about reward scheduling. Performing the Stroop task requires cognitive control; saying 'no' to a cookie requires self-control. We lament that the debate surrounding 'ego-depletion' [113] has made it difficult to discuss the connection between metabolic resources and cognitive processes. We do not remark on whether self-control is a resource with metabolic limits (see [102] for a recent meta-analysis), but we do claim that cognitive control is limited, as is borne out by ample evidence.

The computational model we propose also sheds light on some longstanding puzzles in cognitive science unrelated to mental effort. We have argued that each task requires the development of a probability distribution over transmitted signals, or stimulus 'states', and have shown that this distribution improves with exposure to the task, that is, with practice (see Chapter 3). With improved distributions come improved response times. In learning a task, there are (at least) two distinct types of learning:

learning a policy or stimulus-response mapping, and learning the probability distribution of task-related stimuli. Learning a policy increases subject accuracy; learning the stimulus distribution takes longer, and produces improvements in response times long after accuracy saturates. Tailoring an estimated stimulus distribution carefully to a given task has an interesting downside: it will not be useful in performance of other tasks. In effect, we predict a general lack of skill transfer between learned tasks, a phenomenon that has puzzled researchers from Thorndyke (cited in [144]) to researchers validating more modern 'brain training' regimes.

Finally, we comment briefly on the relationship between our current discussion and the distinction made between 'fast and slow' [158] or 'procedural vs deliberate' [79] thinking. 'Fast' or 'procedural' thinking is often identified as utilizing learned stimulus-response mappings, in contrast to the 'mental simulation' of a 'world model' [159] used in deliberate thinking. While this framing is useful and has been experimentally validated to a large degree, it does not account for the phenomena associated with cognitive control and mental effort cited here. In many of the laboratory tasks used to induce mental effort, such as vigilance tasks, the N-back task, or the Stroop task, the instructions are clearly explained to subjects, and subjects are often given enough practice to meet baseline performance levels before experimental data is collected. In other words, the subject is given a 'policy', and need not invoke any 'world model' or mental simulation in service of these tasks. According to the fast-slow dichotomy, these tasks should be fast, procedural, and easy. Nevertheless, the tasks are effortful and fatiguing. We maintain that an information-theoretic quantification of the task requirements is the missing explanatory piece of the puzzle.

Chapter 6

Cognitive cost as the dynamic allocation of energetic resources

6.1 Overview

It is widely suggested that thinking is somehow costly, involving cognitive effort and producing mental fatigue. Often these costs have simply been assumed to exist. Alternatively, they have been characterized as the brain's assessment of lost opportunities, or suggested to be metabolic but with implausible biological bases. We present a model of cognitive cost based on the novel idea that the brain senses and plans for longer-term allocation of metabolic resources by conserving neural activity. With it, we show how a control-theoretic model that constrains decision-making within an energy budget can explain cognitive effort avoidance in terms of an optimal allocation of limited energetic resources. The model accounts for both subject responsiveness to reward and the detrimental effects of hypoglycemia on cognitive function. A critical component of the model is using astrocytic glycogen as a plausible basis for limited energetic reserves. Glycogen acts as an energy buffer that can temporarily support high neural activity beyond the rate supported by blood glucose supply. The published dynamics of glycogen depletion and repletion are consonant with a broad array of phenomena associated with cognitive cost. Our model thus subsumes both the "cost/benefit" and "limited resource" models of cognitive cost while retaining valuable contributions of each. We discuss how the rational control of metabolic resources could underpin the control of attention, working

memory load, cognitive lookahead, and model-free vs. model-based policy learning. The text and images in this chapter are a modification of work published in [160].

6.2 Introduction

Cognitive processes that require vigilance, model-based lookahead, or extensive utilization of attention or working memory are said to incur a cost [73], are called 'aversive' [71], and are characterized as computationally expensive [161]. General avoidance of such processes makes us "lazy organisms" [162] and "cognitive misers" [163], who in many circumstances would rather use "fast and frugal" heuristics [66] or habits [161] than "intrinsically costly" deliberative thought [164]. Echoing Solomon's "law of least effort" [165], Balle suggested that humans follow a "law of least mental effort" [67], always seeking the least cognitively expensive way of achieving a goal.

Such claims raise the question of *why* certain types of cognition are costly. What, exactly, is being spent? Botvinick and colleagues have suggested that cognitive leisure has inherent value, and that we forego this value by engaging in laborious cognitive processes [164]. A recent paper by Kurzban et al. proposes that focusing limited cognitive resources on a single task to the exclusion of other possible tasks carries an opportunity cost [12]. In this model, a subjective feeling of fatigue is a signal to switch to more worthwhile tasks. Kool and Botvinick propose that the avoidance of cognitive demand is a fundamental principle of cognition, though the authors fail to specify why cognition should be demanding [73]. These approaches are sometimes called economic or "cost/benefit" models of cognitive cost, as they model subject behavior as attempting to optimally trade costs (leisure, opportunity cost, cognitive demand) for benefits (reward, leisure).

"Cost/benefit" models provide an explanation for the finding that increasing reward in specific types of tasks can induce subjects to exert more cognitive effort [166, 167] and improve executive function [168]. A pernicious drawback of "cost/benefit" models is that they decouple the act of cognition from its fundamentally limited biological substrate, the brain. As such, they are unable to convincingly account for the *dynamics* of cognitive exertion and mental fatigue. "Cost/benefit" models are also fundamentally divorced from the well established connection between blood sugar levels and cognitive

function, a relationship familiar to every doctor and diabetic. As the blood sugar level of an individual falls, precisely those processes that are considered costly are first affected [112].

Another influential approach links cognitive costs to the utilization of a limited resource, presumably blood glucose [114]. In this model, use of costly processes diminishes available glucose, leaving less fuel for future processes. Proponents of this assumption typically focus on self-control, one instantiation of top-down executive control over behavior. In the frequently used "dual-task" paradigm, subjects are asked to perform an initial "depleting" task involving extensive use of self-control. They are then asked to perform a second demanding task. A commonly reported finding is that subjects perform worse on the second task *only if* the first task was sufficiently demanding, and the performance decrement can be eliminated by offering subjects a glucose drink [114]. Unlike "cost/benefit" models, "limited resource" models offer no mechanism by which motivational factors can influence subject behavior. Additionally, reported blood sugar decreases arising from cognitively demanding tasks (as reported in [111, 114]) are much smaller than the changes required to effect task performance. Finally, the strength of "limited resource" findings are coming under increasing scrutiny from post-hoc analyses [99, 169].

In this chapter, we introduce a new model that treats cognitive resources as depending squarely on a metabolic substrate with explicitly specified dynamics, while still allowing for the possibility of motivational factors to alter agent performance. We suggest that an individual's decision of whether or not to incur cognitive costs in a given situation can be fruitfully understood as one of decision making *strategy*: an agent will only commit limited resources in cases where the payoff is worth it. Unlike "cost/benefit" models, however, we treat resources as dynamically utilized and replenished. Much like a marathon runner, an agent attempting to optimize long-term performance may choose to purposefully limit exertion in order to maintain resource reserves for future use. What may *appear* to be aversion to cognitive effort may in fact be strategic resource allocation.

A view of the brain as engaging in cognitive strategy selection that is dynamic, constrained, and which maximizes a objective function is naturally modeled using optimal control theory. Using an optimal control theory framework allows and requires the

modeler to be explicit about the dynamics of the system being modeled, the objective function to be optimized, and the planning horizon of the agent. From this perspective, assumptions of limited resources and cost/benefit tradeoffs are not diametrically opposed, as some have suggested [12], but are different components in a more general framework. So-called "opportunity costs" are simply a special case in which an agent has more than one task available to choose from. The "limited resource" assumption is a special case in which system dynamics are specified but in which no explicit claim is made about what is being optimized.

In what follows, we provide an optimal control model of energy use in the brain. The model provides a novel explanation of cognitive costs as arising from intelligent resource allocation over time. We briefly review evidence supporting our specification of system dynamics, objective function, and controls. We then discuss results from a computational implementation of our model, and compare the effects of various modeling assumptions. Finally, we discuss the implications of our model and suggest directions for future work.

6.3 Dynamic resource control

6.3.1 Background

Optimal control theory is a mathematical approach to optimizing dynamic action selection. Given a system with intrinsic dynamics, a controller repeatedly receives signals from the system, estimates its state, and executes actions in order to optimize an objective function over time. We develop the hypothesis that the brain has an intelligent control system for managing its use of metabolic resources by trading off performance for reductions in neural activity. First we review the evidence for a control system view of energy management in the brain and then develop a mathematical model of the same.

Cognitive fatigue and cost as energy depletion

Human cognition is a biological process operating within biological constraints. As such, it is not surprising that hypoglycemia is known to cause performance decrements in cognitive tasks. Moderate hypoglycemia, such as that arising from fasting, can impair

cognitive performance in short term verbal [170] and spatial [171] memory, and the speed of mental computation [172, 173, 122]. More severe hypoglycemia has been shown to negatively affect performance in the Stroop task [174], multi-choice reaction time tasks [174, 175, 176], the PASAT mental arithmetic task [175, 177], digit span tasks [178, 179], the Tail Making B task [180, 181, 175], tracking performance [176, 180], attentional tasks [182, 183], driving [184], and auditory processing [181], though some studies report contradictory findings [185, 186, 182, 187] and high individual variation in effects [174, 180]. In general, performance in tasks requiring only simple motor functions (like the Finger Oscillation Test and Finger Tapping Task) are not affected [186, 177]. Providing subjects a glucose drink after fasting can improve performance [170, 171, 188, 186, 187]. Similar improvement was not found when subjects were given a sweetened placebo in place of a glucose drink to raise blood sugar levels [188, 189, 190]. Some studies report decreased reaction time while others reported decreased accuracy. We suspect that these differences can be explained by specifics of task design and reward structure, though there is some evidence for an effect of individual differences during mental fatigue [174, 180]. See [112] for a thorough review on the effects of glucose levels on cognitive function.

Subjective mental fatigue and time-on-task can produce similar performance decrements to hypoglycemia [191, 192]. As mentioned above, proponents of the "limited resource" account of cognitive costs observe that the dynamics of cognitive fatigue and performance degradation is consistent with the depletion of a limited resource. That resource is largely assumed to be blood glucose. However, direct measurement of blood sugar levels [111, 193] and metabolic rate [194] during cognitively demanding tasks show effects that are too small to account for the detrimental effects on performance that occur during a hypoglycemic state. We suggest that this apparent contradiction can be explained by accounting for the energy storage and buffer mechanism provided by astrocytic glycogen, in which glycogen is the limited, depleted resource. If this is the case, glycogen-dependent neural activity should suffer when glycogen is depleted, while extended cognitive load would have little or no effect on overall blood glucose levels.

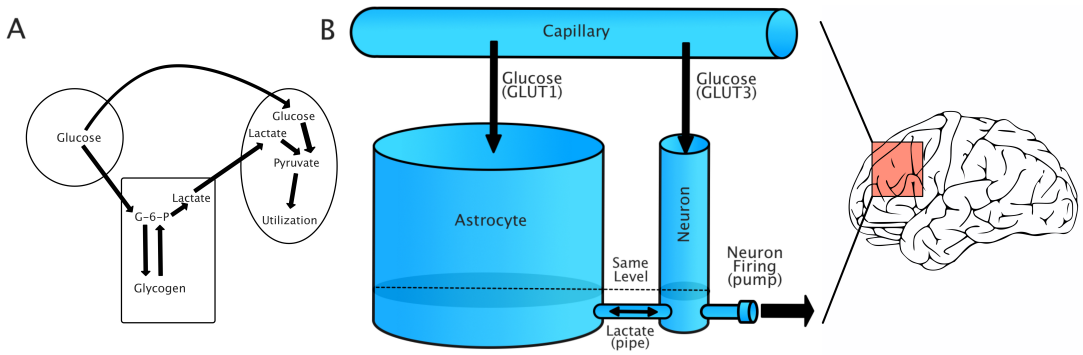


Figure 6.1: Energy flow between capillaries, astrocytes, and neurons. (A) Simplified account of capillary/glycogen/astrocyte relationship, modified from [198]. (B) A schematic of our model, in which energy is treated as a single fluid flowing between compartments. Lactate/GLUT labels are only for reference, as our model treats energy flow as the flow of a single fluid. The model should be understood to represent dynamics in a small region of the brain that has relatively uniform energy dynamics.

Brain glycogen as depletable energy resource

Glycogen is a storage form of glucose. In the human body glycogen is primarily found in liver and muscle cells, but a small amount also exists in astrocytes. It has been estimated that glycogen metabolism in astrocytes accounts for only 1-6% of energy use in the brain under normal conditions [195]. Despite the small amount of glycogen utilization, the amount of glucose stored in brain glycogen is thought to be greater than the amount of non-glycogenic glucose in the brain ([196], cited in [197]). Moreover, studies of both *in vivo* and *in vitro* glycogen metabolism show that its usage is critically linked to periods of neural stimulation.

Figure 6.1A shows a simplified schematic of the relationship between capillaries, astrocytes and neurons. Glucose from capillaries is transported to astrocytes and neurons via facilitative glucose transporter proteins (GLUT1 for astrocytes and GLUT3 for neurons). Glucose is phosphorylated to glucose-6-phosphate upon entering an astrocyte. From there, it can be either stored as glycogen or converted to lactate. Lactate is transported from astrocytes to neurons using monocarboxylate transporters [199].

In a series of *in vitro* experiments, Brown and colleagues investigated the dynamic relationship between astrocytic glycogen and action potentials in the mouse optic nerve in the presence and absence of glucose [200]. See Figures 6.2A and 6.2C for plots of

the relevant dynamics. Axonal response to stimulation was measured using compound action potential area, or CAP area. When glucose was removed from the environment and neural tissue was stimulated, CAP area remained robust for up to 20 minutes, during which time glycogen stores in astrocytes decreased in a remarkably linear fashion. Glycogen content of astrocytes was strongly predictive of the duration of sustained activity following aglycemia (see Figure 6.2C). In addition, inhibiting monocarboxylate/lactate transfer caused CAP area to decrease sharply rather than remains stable, while introducing lactate sustained CAP area when glycogen was absent. These observations strongly indicate that astrocytic glycogen acts as a supplementary fuel reservoir for neuronal activity. Moreover, in the presence of normal glucose levels, axonal stimulation still led to a (less rapid) drop in astrocytic glycogen levels, indicating that glycogen is utilized even in the presence of a normal concentration of glucose. Finally, CAP area was maintained when lactate transport was blocked and a high concentration of glucose was present, but not when the concentration of glucose was low, indicating that neurons also use glucose directly (see [200] figure 3C, also [199]).

The link between neuronal stimulation and glycogen utilization is supported at a larger scale by in research involving animal models. Choi et al. subjected rats to insulin-induced hypoglycemia [201]. As brain glucose approached zero, brain glycogen content (as measured using 13-C NMR) declined gradually and sustained brain activity for two hours. Glycogen utilization has also been shown to increase by tactile stimulation of rats [202, 203, 204].

Glycogen stores have been shown to increase during sleep [202], anesthesia and sustained levels of high blood sugar [205], and to decrease during sleep deprivation [206]. Glycogen accumulates faster in regions of the brain that have highest synaptic density [207] and has a high concentration in the cerebellum, hippocampus, thalamus, and striatum [208]. Finally, glycogen does not appear to be a passive reservoir, utilized only when energy need exceeds resources. Glycogen can be synthesized and degraded simultaneously [209], and glycogen turnover rate increases in the presence of nearby neural activity [210, 203]. Taken together, current evidence strongly suggests that astrocytic glycogen acts as a energy shunt or reservoir that is depleted during periods of high neural activity and repleted during rest, a shunt into which energy is consistently being deposited and released. This stored energy can support neural activity that exceeds the

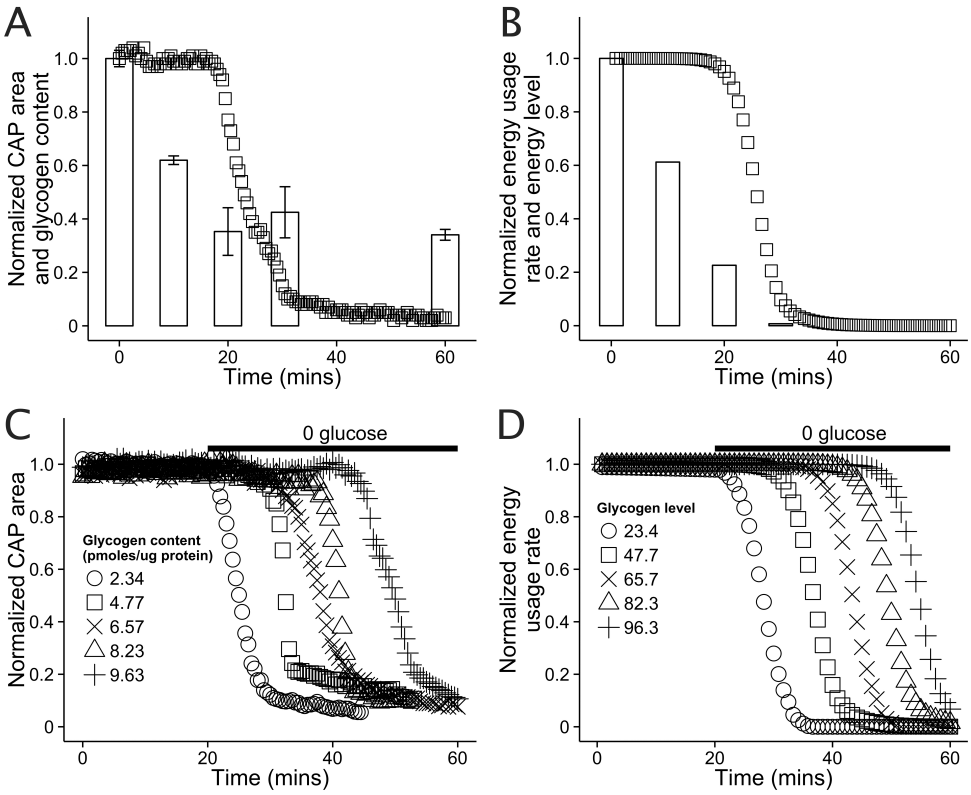


Figure 6.2: Comparison of energy dynamics used in our model (right) with experimental data (left). (A) Recorded CAP area in a mouse optic nerve (squares) and glycogen content (bars). The nerve was stimulated in a solution with no glucose. Note that glycogen is not further depleted after reaching $\approx 25\%$ of its original level. Figure recreated using data from [200]. (B) A simulation of the same situation as (A) using our model. To simulate aglycemic conditions, the energy flow from the capillary, E_B was set to 0 for the duration of the simulation. (C) Recorded CAP area in the mouse optic nerve in vitro as a function of time and the initial glycogen content in nearby astrocytes. At 20 minutes, the solution was replaced with a solution containing no glucose. Figure replotted using data from [200]. (D) A simulation of the same situation as (C) using our model. The absence of glucose in solution was modeled by again setting $E_B = 0$ at 20 minutes. In our model, astrocytic energy level ranges from 0 to 100, arbitrary units.

instantaneous resources of available glucose, and is replenished during rest.

6.3.2 Optimal control

An optimal control problem is fundamentally defined by system dynamics, controller sensors, and an objective function. In the model we present, energy resources in the brain have intrinsic dynamics and represent the system to be controlled. The system state consists of the resources available in different areas of the brain, namely the energy residing in astrocytes, and neurons. The system dynamics describe energy flow between capillaries, astrocytes and neurons within an area. Control of the system takes the form of increasing and decreasing energy usage rate. In neural terms, we interpret this control as the change in concentration of some excitatory neuromodulator. An increase in neuromodulator concentration increases neural excitability and the recruitment of more active neurons, with which task-related energy utilization increases linearly. Actual neural recruitment and associated energy utilization depends on available resources, so the energy flow out of neurons is a function of both the excitatory concentration and available energy. The population of recruited neurons maps to performance using a task-specific performance curve (see Figure 6.3).

In an optimal control problem, a controller attempts to optimize an objective function (also called an objective function) over time. We assume that the objective function includes rewards given for task performance. Whether the objective function should include cognitive costs (indeed, the very phrase "cognitive costs" belies the implication) is an open question. The received wisdom is that cognitive costs are something to be avoided for their own sake - that is, they belong in the objective function. We suggest the possibility that apparently "costly" cognitive processes are instead avoided because they strongly affect energy resource availability, and hence performance at longer time scales. If an agent has the capacity to plan, they may judiciously use resources in order to maximize reward over time. Indeed, the model we propose herein suggests a method for discerning whether cognitive costs can be said to exist per se (see Section 6.4.1).

Our proposed mapping between the optimal control framework and brain energy dynamics is given in Table 6.1. The goal of the controller is to execute a sequence of control actions that minimizes the objective function over a given time horizon. The objective function J, shown in Equation 6.1 for a time horizon n and initial state x_0, is

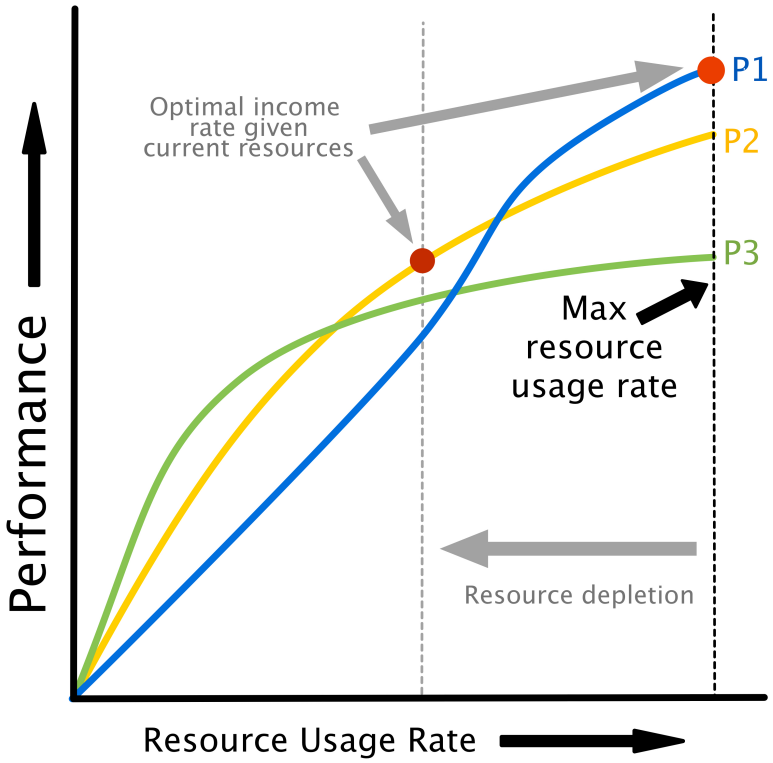


Figure 6.3: Different curves can represent either different policies/strategies for the same task or different tasks. Note that as resources are depleted, the maximum possible energy utilization rate drops (see Figure 6.4C), creating the possibility of a different strategy or task being optimal based on energy dynamics alone. This provides a natural explanation for task or strategy switching as a result of fatigue.

Control theory	Variable	Interpretation
Time index	k	Index of time at a scale in which distinct control actions are possible
State	$x_k = [H_N, H_A]$	Quantity of energy available to neurons and astrocytes
Control	u	Neuromodulator concentration driving neural recruitment in an area
Dynamics	$x_{k+1} = f(x_k, u_k)$	Energy dynamics in the brain
Objective function	$g(x_k, u_k)$	Combination of cognitive costs (if any) and rewards for a single time step
Overall cost	J	Overall objective to be optimized within a given time horizon

Table 6.1: Proposed relationship between a control theoretic framework and the optimization of energy use in the brain over time.

additive in that it is the sum of costs at each time step k.

$$J(x_0) = E\left\{\sum_{k=0}^{n} g(x_k, u_k)\right\} \tag{6.1}$$

Energy dynamics operate at varying temporal and spatial scales. The model we introduce in the present work is intended to represent neural dynamics on the time scale of roughly 20 minutes to several hours, as that is the time scale of glycogen depletion and subjective mental fatigue. The spatial scale of our model is a local brain region with homogeneous energy resources, subserving some particular cognitive function. Elsewhere in this chapter, we consider cognitive functions like working memory, executive control, and attention to be candidate functions as they are sensitive to both energetic resources and reward, but in the present model we treat only a simplified cognitive function whose utilization maps to performance in a 1-dimensional manner. This function is intended to be the simplest case of an energy- and reward-sensitive cognitive function, and more investigation is needed to understand how specific functions like attention or working memory should be modeled. We envision energy dynamics being regulated across several regions (and functions) at longer time scales, however, here our goal is to develop an area-specific control model whose extension to the full brain via

hierarchy and composition is the subject of future work.

We model the task-related dynamics of energy use using a compartmental fluid flow model and show that our model is consistent with available data. We then show how neural activity can be modulated to control metabolic usage and maximize long-term task performance.

Dynamics model

We use glycogen-supported energy transfer as a dynamics model in our optimal control approach to modeling cognitive costs. As we are at present introducing a model that we hope is *qualitatively* useful, we will use a greatly simplified model of energy flow from capillaries to astrocytes to neurons. Astrocytic glycogen and glucose is treated as one energy pool, and neuronal lactate and glucose is treated as another.

The model we propose is illustrated in Figure 1B. In this model, energy (in the form of glucose) flows from capillaries to both astrocytes and neurons. We model energy flow as a fluid flowing from capillaries into astrocyte and neuron "buckets" connected by a pipe. Though molecule transfer occurs via transporter-facilitated diffusion, we make a simplifying assumption and model the transfer of energy as the flow of a liquid though containers, constrained only by the "radius" of connecting pipe. Liquid flow between the two buckets is governed by the Torricelli Model, in which the change in height of the fluid in a bucket is proportional to the square root of the fluid height. Each bucket is treated as "leaky", leaking into the other bucket.

The fluid flows from a capillary reservoir to both neurons and astrocytes at a certain rate. Astrocytes are modeled as having a greater energy/fluid capacity than neurons. Energy can flow freely from astrocytes to neurons and back via a pipe at the base of both containers (this models lactate transfer between cells). Fluid levels naturally move toward equilibrium in connected vessels. Energy/fluid can flow out of neurons via a variable rate active pump. The requested rate of pumping, or energy utilization, is the single control variable of the system.

The modeled relationship between requested energy utilization and actual utilization is not linear. If the level of energy in a neuron is zero, clearly no energy is present to be utilized. Inspired by dynamics illustrated in [200], we model the relationship between requested energy utilization and actual energy flow as a bounded exponential. The

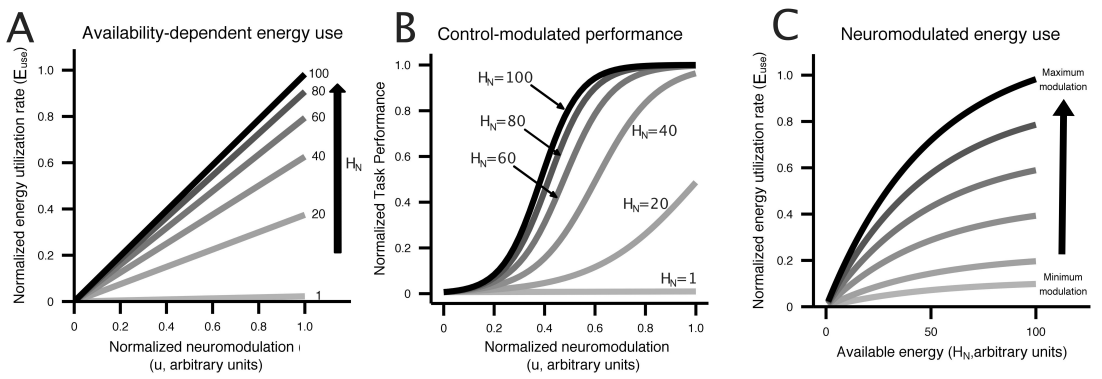


Figure 6.4: Visual display of the relationship between control/neuromodulation (u), energy availability (H_N), energy use (E_{use}), neural recruitment ($NeuralRecruit(x,u)$), and performance ($Perf(x,u)$). Curves were generated using the equations from 6.5 and parameters from Table 6.2. (A) The relationship between control/neuromodulation and energy utilization is modeled as linear, with the slope controlled by the amount of energy available to neurons. (B) Performance as a function of control/neuromodulation on a specific task at different levels of energy availability. This figure illustrates that the same performance can be achieved with different levels of available energy through the application of varying levels of control/neuromodulation. (C) Energy utilization has an upper bound and is affected by both control/neuromodulation and energy availability.

actual energy utilization rate depends on both the energy level in the neuron and the requested rate. This relationship is illustrated in Figure 6.4. The combined dynamics equations are shown in equation set 6.3.

$$\begin{aligned} x_{k+1} &= f(x_k, u_k) \\ x_{k+1} &\approx x_k + \frac{dx}{dt}(x_k, u_k)\Delta t \end{aligned} \tag{6.2}$$

where dx/dt is the differential change in the state given by

$$\begin{aligned} \frac{dx}{dt} = \begin{bmatrix} dH_A/dt \\ dH_N/dt \end{bmatrix} &= \begin{bmatrix} \text{Between-compartment flow} + \text{Inflow from capillaries} \\ \text{Between-compartment flow} + \text{Inflow from capillaries} - \text{Outflow} \end{bmatrix} \\ &= \begin{bmatrix} \frac{a_{connector}}{a_A}\sqrt{|H_N - H_A|}\cdot(H_N - H_A) + \alpha E_B \\ \frac{a_{connector}}{a_N}\sqrt{|H_A - H_N|}\cdot(H_A - H_N) + \beta E_B - E_{use}(u, H_N) \end{bmatrix} \end{aligned} \tag{6.3}$$

The energy outflow E_{use} is a function of energy demands due to the neural excitability control level u and the current neural energy availability H_N.

$$E_{use}(u, H_N) = \gamma u(1 - e^{-\delta H_N}) \tag{6.4}$$

Each of the model parameters has a simple interpretation:

- H_A, H_N: amount of energy in astrocyte and neuronal compartments, respectively modeled as fluid heights.
- u: energy outflow "demand" due to neural activity. This is akin to neuromodulator-induced neural recruitment in the brain, modulating energy use with task demands.
- $E_{use}(u, H_N)$: energy outflow rate as a function of demand and availability. This relationship is modeled as a bounded exponential to account for both a zero rate of flow for an empty compartment and an upper bound of energy utilization.
- a_A, a_N: energy capacity of astrocytes and neurons, respectively.
- $a_{connector}$: parameter controlling the energy flow rate between the astrocyte and neuron compartments.
- α, β: parameters controlling the energy flow rate from the capillary to the astrocyte and neuronal compartments, respectively.
- γ: scaling parameter controlling the utilization of energy as a function of neuron energy level.
- δ: parameter controlling the sensitivity of energy use to low energy availability.
- E_B: energy content of the blood. Used to modulate the overall flow of energy into the neuron and astrocyte buckets and simulate hyper- and hypoglycemia.

Cost model

The goal of the controller is to optimize the objective function over a given time horizon. Each time step k is an instance at which controls can be executed. The time scale is

intrinsically set by the system dynamics. In our case, it is the time scale at which an agent can change its level of cognitive effort. This is not necessarily the same as the time scale of a given task.

The relationship between attempted cognitive control u, resource availability $[H_N, H_A]$, and performance is illustrated in Figure 6.4. Cognitive control is mapped to task performance in a two step process. First, requested control is converted into actual energy utilization in a fashion that depends on the amount of energy available to neurons. Energy utilization is assumed to reflect neural recruitment for a particular task, which could affect working memory load, attention, vigilance, or any other cognitive resources that are variable and contribute to task performance. Then, energy utilization is mapped to performance through a task-specific performance curve. Example performance curves are shown in Figure 6.3. Each line represents a possible relationship between resource utilization and performance for a given task, or different strategies on a single task.

Our model assumes that resources can be utilized at a rate dependent on the available energy level. If different tasks or strategies are available as in Figure 6.3, an agent might change tasks or strategies (or "policies", in the terminology of optimal decision making) in order to maintain optimal performance. The availability of a set of performance curves dependent on resource levels, whether they represent tasks or different strategies for the same task, provides a natural explanation for task and strategy switching that does not rely on theoretical constructs like "opportunity costs".

Equation set 6.5 represents the control-to-performance relationship at time step k. The cost $g(x, u)$ for a state-control pair is calculated to be a linear combination of the control u and task performance (which is assumed to translate directly to reward).

$$\begin{aligned} g(x,u) &= \lambda u - Perf(x,u) \\ Perf(x,u) &= \frac{1}{1+e^{-NeuralRecruit(x,u)}} \\ NeuralRecruit(x,u) &= \gamma_e E_{use}(x,u) + \gamma_f \\ E_{use}(x,u) &= \delta u(1-e^{-\gamma H_N}) \end{aligned} \tag{6.5}$$

where $Perf$ is the performance curve relating neural recruitment and energy consumption to task performance. $NeuralRecruit$ represents the population size recruited given the energy use. Parameter values in γ_e and γ_f were chosen to make the variable part

of $Perf$ have the same scale as the glucose usage E_{use}. The control component of this sum is represented by the λu term.

When $\lambda > 0$, the control variable u influences the objective function, in which case cognitive control can be said to be intrinsically costly. While we expressed costs in terms of control (which is traditional for optimal control theory), we could have equivalently used the linear relationship between u and energy use, to express the costs in terms of energy use, or nonlinearly in terms of neural recruitment. Thus, λ represents both a gain on control cost and a unit conversion factor. We explore the implications of different values for λ in Section 6.4.

6.3.3 Model discussion

Energy dynamics in the brain can be understood to operate at several temporal and physical scales. At the smallest scale, glutamate must be rapidly ($\approx$ 10ms [211]) sequestered following firing to prevent glutamate toxicity. This operation is performed much more quickly than increased regional cerebral blood flow and is thought to be powered by the rapid utilization of astrocytic glycogen (see [212]). At the scale of minutes and hours, high levels of neural activity deplete glycogen stores. This is the scale at which our model is focused. Blood glucose concentration is affected by exercise and food consumption. In our model, the flow of energy from capillaries to astrocytes directly affects the replenishment rate of glycogen (modeled as energy level in the astrocyte bucket). Flow from capillaries to astrocytes and neurons limits the maximum neuronal firing rate following glycogen depletion, in which case energy is utilized as soon as it enters the neuron bucket from the astrocyte bucket or capillary.

As mentioned above, the proposed model allows for a simple explanation of activity-induced cognitive deficits reported in the ego depletion literature. Baumeister and colleagues propose a resource-depletion framework in which self-control (and possibly other cognitive functions) deplete a limited resource [193]. They suggest that this resource may be blood glucose [193, 114], citing the common finding that a meal or glucose drink eliminates cognitive or self-control deficits that follow a demanding task. Instead, we propose that it is *glycogen* stores that are depleted in the presence of sustained cognitive effort. In the absence of increased blood sugar levels, performance should suffer following glycogen depletion. On the other hand, increasing blood sugar levels increases

instantaneous transfer of glucose from capillaries to astrocytes and neurons, providing energy to support normal levels of firing even in the case of glycogen depletion.

Glucose in the blood is treated as an infinitely large resource pool from which resources are extracted at a set rate. In principle, blood glucose could be modeled as a finite pool larger than that of astrocytes. With the exception of Brown (2003) [200], few results exist detailing glycogen dynamics on the time scale of our model, and for this reason model parameters were selected to match glycogen dynamics results found in that paper. A comparison of our model dynamics in hypoglycemic conditions with mouse optic nerve data from [200] can be seen in Figure 6.2. The figures highlight the effect of varying astrocytic glycogen content on the duration of sustained neural activity.

Costs

Researchers have observed for decades that certain cognitive functions are aversive [40], necessitating in turn that humans exhibit a tendency to rely on habits [161] or heuristics [66] to perform tasks. Many suggestions have been made as to the nature of the cost driving cognitive aversion: for example that cognitive effort requires foregone leisure [164], that cognitive costs are a form of opportunity costs [12], or that costs are related to the need for extensive cognitive processing [73, 71].

Despite widespread agreement that cognitive effort is aversive, very little work has been done to quantify this aversion. We propose that a useful way to quantify aversion is in terms of foregone reward. The ability of incentives to induce task engagement is a standard operating assumption in experimental psychology and neuroscience. Extrinsic monetary or caloric reward is only one type of reward and is often compounded by and competes with other extrinsic (social, sexual) and intrinsic (curiosity, empowerment, mastery) rewards for impact on decision outcomes. However, it is easily quantified and has been shown to impact cognitive effort (see [166] for a review). We therefore restrict our treatment of reward to extrinsic reward for task performance (e.g. monetary), though other reward types could in principle be accounted for.

Reward and cognitive effort appear to balance in some way, resulting in a decision regarding whether or not to deploy effortful cognitive strategies. To our knowledge, only one group has attempted to quantify aversion to cognitive effort in terms of foregone reward. Braver and colleagues rewarded subjects for completing an N-back task [65].

After an initial familiarization phase, subjects could make choices of whether to complete a more difficult task (higher N) for more money, or a less difficult task (lower N) for less money. Subjects were explicitly told that reward was contingent on maintaining effort rather than performance. In this way, the researchers effectively determined the amount of money subjects were willing to forego in order to avoid a cognitively demanding increase in N. They found that the subjective value of each level of N, or the amount by which increasing N decreases the preference for an offered reward, decreased linearly with the magnitude of N. These results are fully consistent with the additive objective function, although we suspect a more complex objective function will be needed as experimental results become rich enough to invalidate a linear approximation. However, the deeper implication is that for difficult tasks, by suitably increasing the offered reward the subject will eventually overcome task aversion and attempt the task. For a recent review of neuroeconomic approaches to understanding cognitive effort, see [127].

Controls

By treating cognitive effort as a resource control problem we are assuming the brain has mechanisms that allow control of cognitive effort and that varying effort affects subsequent reward. We believe there are limitations on both the ability to control resource allocation as well as limits on the impact that effort has on performance. Evidence suggests that cognitive effort can increase performance in certain tasks but not others. Camerer and Hogarth reviewed research investigating the relationship between financial incentives and performance in experiments. Their findings were nuanced [166]. Higher incentives do not appear to improve performance in a wide range of task types, including tasks requiring insight (an "ah-hah! moment"). Incentives can consistently harm performance in judgment and decision making tasks in which expert judgment can routinely be out-performed by a simple rule based on quantifiable observations. In this type of task, incentives appear to induce subjects to expend greater deliberative effort, weighting their own (inaccurate) judgements more highly than the predictions of formulas. To be clear, in these tasks incentives appeared to increase effort, but *not* objective performance. One simple way to reconcile these results is to assume the existence of both model-based high-cost deliberative neural computations and low-cost model-free experience-based paths [79], with the switch to deliberative decision-making

resulting in a reduction in performance in cases where model-free solutions are superior.

In addition, incentives are most likely to improve performance in a subclass of judgment and decision making tasks, specifically tasks that are "effort-responsive." These tasks critically depend on the cognitive functions which are the strongest candidates as controllable resources. In tasks where these functions operate, extrinsic motivation can "improve recall of remembered items, reduce the effect of anchoring bias on judgment, improve some kinds of judgments or predictions, improve the ability to solve easy problems, and also sharpen incentives to make zero-profit trades in auctions or do piece-rate clerical work" [166]. These tasks share a reliance on the use of executive function and working memory resources. For our purposes, the important finding is that in a specific but useful set of task types, monetary incentives can explicitly increase the utilization of the exact cognitive faculties that are considered cognitively costly.

There is currently insufficient data to enable us to identify a specific molecular mechanism for the proposed control. However, given the aforementioned connections between metabolic resource levels and offered reward on the one hand, and subject effort and performance on cognitively demanding tasks on the other, it is reasonable to posit the existence of some signal by which neuronal gain is modulated according to both the availability of metabolic resources and reward signals. One proposal for such a signal is some subset of neuromodulators associated with behavioral vigor acting on local excitatory neural gain via glutamate and glycine, though future research is needed to confirm this hypothesis. Botvinick and Braver (2015) provide a review of the possible neural mechanisms of cognitive control, and suggest dopamine as a candidate control signal [213].

Model

The control variable in our model is a brain region-specific increase in neural excitability which we assume serves to recruit more neurons and consume more energetic resources. This control can also be understood as a requested size of a neural population dedicated to a particular task, with the request coming in the form of some excitatory neuromodulator. This control mechanism is compatible with modulation of attention [214], and probably working memory. However, we also acknowledge that there is an excellent case for an alternative mechanism for cognitive control by switching between

decision making systems or policies that differ in costs and performance but can solve the same task. Many recent models of cognitive effort take this approach and simplify the graduation in cognitive effort into two categories of decision-making processes such as "System 1" and "System 2" [215], procedural and deliberative [], or model-free and model-based [79] (for a review of dual-process models of decision making, see [216]). We believe a complete account of the control of cognitive effort will incorporate both of these control mechanisms (graded neural recruitment and strategy switching), a point we return to in the general discussion.

An important implication of interpreting the cost as something to be minimized *over time* is that agents optimizing Equation 6.1 are not myopic: an agent may choose an action that decreases an instantaneous reward in order to maximize reward in the long run. In the context of cognitive costs, there are two basic possibilities:

1. An agent avoids demanding cognitive processes because they are intrinsically costly. In this case the use of such processes would be explicitly represented in the objective function. This is the approach implied by McGuire and Botvinick [71] and elsewhere.

2. An agent generally avoids demanding cognitive processes *because doing so optimizes reward in the long run.*

The second option is analogous to the situation a runner finds herself in when competing in a marathon: sprinting at the beginning of the run is locally optimal but globally disastrous, because this strategy quickly exhausts the limited resources available. Analogously, it is possible that aversion to cognitively demanding processing is not a cost per se, but a strategic use of a limited glycogen reservoir. If this is the case, an aversion to certain cognitive processes may appear to indicate a cost but instead be a long-run performance-preserving strategy. In this case, cognitive costs might not belong in the objective function at all. Our approach encompasses both views, with zero λ parameter in Equation 6.5 for the long-run view, and positive λ for the intrinsic cost view. We explore the predictions made by each of these assumptions in Section 6.4.

Fatigue

In order to effectively utilize control actions, a controller must maintain an estimate of the current state. We propose that a key signal carrying the current energy level maps onto *subjective fatigue*. One might be tempted to suggest that mental fatigue and associated performance decrease is a consequence of resource depletion. Experimental findings contradict this, indicating instead that sufficiently high motivational incentives induce cognitive effort in spite of subjective fatigue [217].

We suggest that fatigue is not a signal of total resource depletion but of impending depletion if the current rate of use is maintained. In other words, subjects feel fatigued when glycogen stores are anticipated to deplete at current usage, and fatigue is a relatively crude signal of partial depletion.

The link between subjective fatigue and partial glycogen depletion has experimental support [218]. Thus fatigue serves as an important signal enabling subjects to estimate their energy state and plan their cognitive strategy accordingly. If immediate incentives warrant further use of a costly strategy, an individual may indeed temporarily continue its use. The implication by critics is that this should be impossible if a resources is in fact depleted and therefore unavailable for further utilization. If fatigue indeed reflects only *partial* glycogen depletion, this criticism becomes irrelevant. We would nevertheless predict that at a long enough time scale, individuals would become fatigued beyond the point of incentives to improve performance because the required resources simply would not be available. While this proposal suggests a global signal for resource depletion, we believe that cognitive fatigue has gradations across brain areas which may produce task-dependent fatigue.

6.4 Simulations

We implemented our model with the dynamics, controls, and costs specified above. The optimal control framework allows (and forces) us to be explicit about an agent's lookahead and the components of the objective function. As mentioned in Section 6.3.3, it is unclear whether aversion to expensive cognitive processes is the result of their being intrinsically costly or simply an effect of long-term strategy. This ambiguity allows us to consider a space of models as indicated in Figure 6.5, with axes representing planning

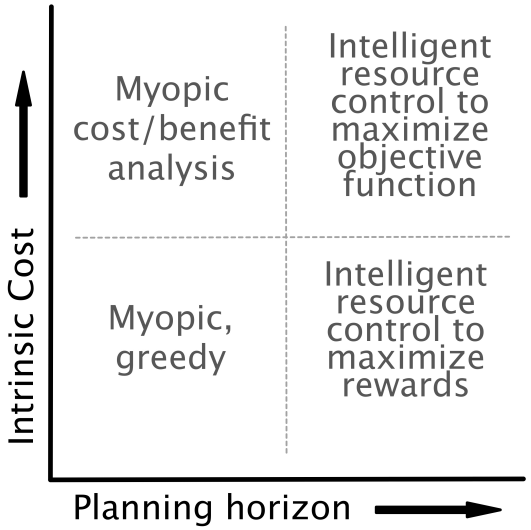


Figure 6.5: Style of behavior depends on lookahead and cost. The model is agnostic as to both the intrinsic cost of control (i.e. whether control is included in the objective function of the optimal control formulation) and the planning horizon of the agent. This flexibility highlights the generality of the optimal control approach. Each choice of planning horizon and intrinsic cost results in an agent with a distinct optimization strategy.

horizon and the intrinsic cost of cognitive effort. On the extremes of the planning axis, we can treat an agent as acting either myopically, with a decision based on only current costs and rewards, or optimally, with a lookahead equal to the time horizon of the task. On the intrinsic cost axis, we can omit costs arising from the cognitive control completely (low costs), or we can include control costs directly in the reward function (high costs). We assume for simplicity that the agent has error-free access to the current state and system dynamics, though in future work we intend to relax this assumption, as these errors may be critical for explaining behaviors that are essentially "illusions of cognitive costs".

Implementation

Optimal control solutions were calculated using dynamic programming for the model in two experiment described below. In both cases the model was implemented with the values for constants listed in Table 6.2.

Name	Value
Initial H_N, H_A	100
$a_{connector}$	0.5
a_A	10
a_N	1
α, β	0.00042
δ	0.05
γ	0.02
γ_e	6
γ_f	5
E_B	100

Table 6.2: Constants used in the computational implementation of the model. For an explanation of parameter values, see Section 6.3.2.

The dynamics used are listed in Equation set 6.3. The objective function for each step k is given in equation 6.5. Each dimension of the state space had a range $[0, 100]$. The state space was discretized to integer values. Transitions were probabilistic based on the fractional part of each dimension of the new state. For example, a value of 2.1 would be discretized as "2" 90% of the time, and "3" 10% of the time. At each time step, control levels were chosen from were chosen from $U = [0.5, 1, 2, 3, 4, 5]$.

A control action was taken at each time step k. The temporal resolution for the dynamics model was higher than that of the control actions, so once a control action was selected, the system was run forward 100 iterations using Euler integration while maintaining the selected control.

The optimal control strategy was calculated using dynamic programming for a discrete state space as described in [219]. To represent the conditions described in Figure 6.5, simulations were performed for lookahead values of 1 and 100. In the first case, the control cost is simply treated as the single state's g function and the control is chosen according to

$$u_{selected} = \underset{u \in U}{\operatorname{argmin}}\, g(x_k, u)$$

With a lookahead equal to the N, the control at each step is chosen recursively according to

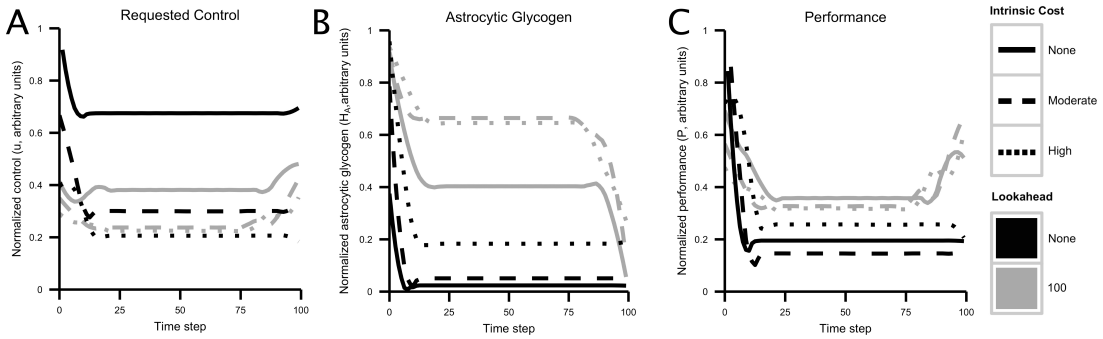


Figure 6.6: Results from Simulation 1, separated by agent lookahead and intrinsic cost (see also Figure 6.5). Each curve represents an optimal control trajectory under the given conditions. As expected, agents with a longer lookahead and lower intrinsic costs exhibit better performance while generally exercising less control (less neuromodulation).

$$u_{selected} = \underset{u \in U}{\operatorname{argmin}} \{g_k(x_k, u) + J_{k+1}\}$$

where J_{k+1} is the minimum cost-to-go from step $k+1$ onward.

Simulation 1

In the first simulation, a finite time horizon of $N = 100$ was used and reward (equal to performance) was assumed to be available for the duration. Optimal control trajectories were calculated for lookahead values of 1 and 100 and for $\lambda = 0, 0.1, 0.4$. The value $\lambda = 0$ reflects the case in Figure 6.5 in which cognitive costs are not included in the objective function. As discretization of the state space led to stochastic state transitions, simulations were run four times and results were combined using LOESS smoothing.

Control, resource, and performance trajectories for each combination of lookahead and λ are shown in Figure 6.6. The simulation results reveal several important patterns. First, a higher control level is sustained when cognitive costs are not included in the objective function $\lambda = 0$. In addition, control strategies that include a lookahead of 100 maintain glycogen levels that are much higher than those maintained by no lookahead. This result reflects strategic resource allocation over time, a feature that is not present with the agent cannot foresee system dynamics in the longer term.

The most important result relating to the discussion above is that when a lookahead is included, the optimal solution is to sacrifice performance initially in order to maximize overall performance. Comparing the initial requested level of control (that is, allocation of neural resources) and resulting performance with the long-term performance curve, one is again reminded of a marathon runner. Without the ability to predict the depletion of resources and its effect of resource depletion on performance, the agent initially requests a high amount of resources. This quickly decreases the level of astrocytic glycogen, which leads to a lower sustainable performance level and overall lower performance.

To rephrase this result in terms used above, what appears to be an initial aversion to cognitive costs is actually a strategic decision to avoid resource depletion and maximize long-term reward.

Simulation 2

In the second simulation, reward was made unavailable for certain periods, simulating conditions where no reward is available to the agent (resting between experimental tasks, for example). The dynamics, parameters, and objective function were identical to those used in Simulation 1, with the exception that the performance function returned 0 for two periods of time, regardless of energy level or control action. The simulation was run five times for 500 steps, and again the results were combined using LOESS smoothing.

Simulation traces are shown in Figure 6.7. Though control was not incorporated in the objective function, the control action was nonetheless moderate throughout the simulation. Control was minimal during the no-reward periods, as expected. That the control does not appear to be a step function at the transition points is due to the smoothing method used. As also seen in Baumeister's dual-task ego-depletion experiments, performance was highest in the first rewarding period and diminished in the second. Though astrocytic energy levels rebounded somewhat during rest periods, the requirement of a minimal level of control ($u = 0.5$ rather than $u = 0$) meant that available energy was never fully replenished. This is in accordance with evidence suggesting that astrocytic glycogen is slowly depleted during waking hours and substantially replenished during a few hours of sleep [202, 206].

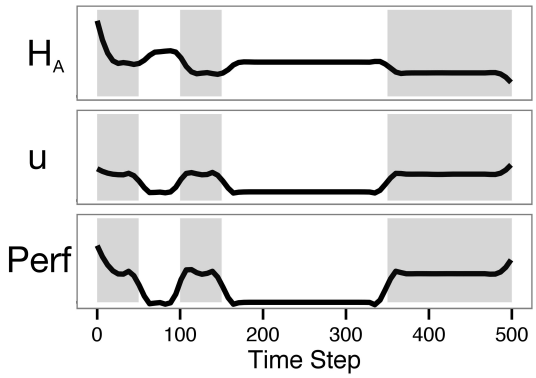


Figure 6.7: Results from Simulation 2, with zero intrinsic cost and a lookahead of 500. Shading indicates periods in which the agent could be rewarded (on-task periods).

Model extensions and future work

As presented here, our model treats energetic resources as an energy flow from capillaries to astrocytes and neurons. The simulations above provide qualitative relationships between control, performance, and energy dynamics. It would not be difficult to calibrate the model in order to match known rates of glucose transfer from capillaries to astrocytes and neurons. The energy flow could be changed to use diffusion equations instead of liquid flow equations. Conversion of glucose to glycogen, then lactate, is somewhat inefficient, and that inefficiency could be included in the model. The agent's state is currently assumed to be perfectly known by the agent, but a more realistic approach would be to have the agent estimate its state from a crude, noisy input. This would reflect our suggestion that fatigue is a signal of partial glycogen depletion. These complicating factors were omitted from the current model to preserve as much simplicity as possible while still providing a useful conceptual framework. Even so, the model already provides qualitatively useful predictions (see e.g. the astrocytic glycogen levels in Figure 6.6B, the performance trajectories in 6.6C and the presence of a performance deficit in subsequent tasks in Figure 6.7).

6.4.1 Testable predictions

Given the model outlined above, there is a way to test whether the cognitive cost parameter λ is greater than 0, that is, whether the objective function in our model

should include a penalty for cognitive control. The planning-based model introduces a tradeoff between current and future resource utilization, with no particular penalty for current utilization over future. In contrast, a cognitive cost of $\lambda > 0$ implies a trade off between costs and rewards in the present with no consideration of the future. These models make different predictions in a condition where a time horizon is short or non-existent (in other words, in which no planning is needed). One way to induce such a scenario is to provide an immediate and abundant source of energetic resources, such that high utilization of astrocytic glycogen is not necessary, even in conditions of high neural activity. To do this, one could clamp an individual's blood sugar to a high level, such that all additional energy utilization arising from demanding cognitive processing is provided from the blood (the capillary-neuron connection in Figure 1B) rather than the astrocytic glycogen shunt. In this condition there are no future energetic consequences to high neural activity. Our model predicts that in such a condition, subjects should not show cognitive cost effects if $\lambda = 0$. In other words, all cognitive effort aversion can be attributed to planning. If cognitive cost effects persist we would conclude that $\lambda > 0$, meaning that cognitive effort should be treated as a cost per se.

The addition of a glycogen energy store allows us to make a prediction that would potentially falsify either our account or the glucose-only "limited resource" account. Suppose a subject were asked to complete a cognitively demanding task, after which their blood sugar were clamped at a low level for a period of time. Results from [200] suggest that astrocytic glycogen would be somewhat depleted during this period (see Figure 6.2). Now suppose subject blood sugar was reverted to normal levels, and they were asked to perform the task again. If performance on demanding tasks, and the associated feeling of effort, depends on the availability of glycogen, we should expect performance on the second task to be worse than initial performance. If, on the other hand, glycogen does *not* act as an energy shunt and all energy is taken directly from blood glucose, performance on the task should be equivalent both times. The subjective feeling of effort could also be compared before and after clamping. This experiment is similar in design to the dual-task paradigm mentioned above, except that it explicitly tests the role of glycogen in task performance and subjective effort.

6.5 Implications

The idea that the brain has a sophisticated controller for resource allocation has a number of important implications that we believe provide a novel explanatory synthesis of a range of phenomena. The timescale of the dynamics of glycogen depletion puts limits on sustained neural activity. It also introduces potentially costly consequences from operating at peak performance in one task on the performance of subsequent tasks. We term controlling resource allocation to optimize long-term performance *optimally lazy*, which amounts to incorporating future resource availability into decisions about how to recruit neural activity to solve a particular task in the near-term. Although we developed our model around the control of neural recruitment, we hypothesize that there may be several important control schemes that operate at higher spatial and temporal scales. The putative control schemes include:

1. Control by modifying gain on neural activity

This control mechanism is the focus of our paper. It optimizes energy consumption on the timescale of a neural population that has shared glucose dynamics and could be the target of a local neuromodulator gain control signal. This control strategy provides a new role for excitatory and inhibitory neuromodulators, and we believe it includes known gain control systems like attention and working memory. We expect to see this type of resource control at the intersection of neural processes that are costly and whose recruitment makes a graded impact on performance. While we modeled these gains at the level of a neural population, it is more likely that gain control is structured hierarchically, with multiple levels of resolution. For example, the concept of *vigor* can be implemented by a more global gain on goal-oriented behavior. Vigor is known to be modulated by resource availability, with rich resource availability increasing willingness to work in humans and animals, and in the speed and variety of behaviors expressed [220].

2. Control by switching strategies or policies with different performance or efficiency trade-offs.

There are also advantages to incorporating knowledge of differential costs of neural activity to learn more metabolically efficient strategies or policies. Investments in effiency have the largest pay-offs in frequently recurring tasks. If model-based look-ahead is indeed differentially costly, then efficiency may drive model-free policy learning. The idea that energetic efficiency drives model-free learning is a significant change of viewpoint. Model-free methods are usually justified on the basis of improved accuracy as experience grows [79, 221]. However, congruent with efficiency driving learning, Huang et al. provide evidence that suggests later stages of motor learning are directed toward increasing metabolic efficiency, without gains in performance [194]. More generally, varying the weight on metabolic costs during task learning can produce a family of solutions that can be rapidly selected between during a task to provide an alternative online control of metabolic costs. Given a family (at least two) strategies (policies) that have different neural costs and performance on the same task, a controller can select (or weight) policies to trade-off performance vs. cognitive costs. The current model allows for this possibility via the inclusion of multiple performance curves, as seen in Figure 6.3.

3. Control by modifying the distribution of glycogen across the brain.

When efficient solutions to recurrent tasks are not available (or take too long to effectively learn), the brain may invest in changing the distribution and quantity of energetic stores across the brain, either by changing locations and numbers of astrocytes and/or the amount of glycogen stored in astrocytes. Reallocation of energetic stores constitutes a distinctive kind of control that serves to anticipate and meet the demands of recurrent neural activity at longer timescales. If present, it would constitute a distinctive type of *endurance learning*, that would provide a basis for generalizable gains in resource dependent cognitive processes like attention, working memory, look-ahead, and executive function. It is also strongly analogous to changes in muscle glycogen stores induced by exercise. Consistent with this idea, hypoglycemia causes lower cognitive/physical performance, and we have a real need for rest after both heavy cognitive exertion similar to physical exercise. The cognitive benefits of physical exercise may result in part from

better metabolic regulation, and cognitive training may produce increases in glycogen similar to the impact of physical training on muscle glycogen. Changes in resources may underlie the pattern of cognitive gains documented in video game players, which show general improvements in visual attention and working memory [222], while simultaneously providing a fundamental reason for the ubiquitous finding of lack of transfer in most learning paradigms. Learning paradigms are almost universally conducted in conditions where task recurrence would encourage the investment in efficient (but necessarily specialized) solutions.

Considering glycogen allocation as an optimal resource allocation problem, we predict that the differential density of astrocytes and glycogen stores across the brain will be a function of the frequency of sustained activity. Areas whose activity are infrequent or short relative to depletion dynamics will need fewer resources than areas whose activity is frequent and sustained. This relationship between the statistics of sustained neural activity and glycogen stores is easily testable. In general, this predicts that the more specific the cognitive function, the less frequent its sustained use and the more susceptible it will be to degradation with decreases in energy availability. As sustained functions are likely recoded in efficient ways to exploit more direct sensory-to-motor mapping, we predict this degradation will fall most heavily on higher cognitive functions. The best evidence for this idea are the patterns of loss of cognitive function with declines in blood sugar, in which working memory, attention and executive control are more sensitive to hypoglycemia than visual and auditory acuity or basic motor functions [112].

4. A mechanism for the integration of energy utilization.

The model presented in this paper requires some mechanism by which the depletion of astrocytic glycogen is translated into effort avoidance behavior. Accordingly, one prediction of our model is that the trajectory of glycogen storage levels should be coded neurally at a larger scale than local negative feedback due to neurotransmitter concentrations. This energy usage information must then be transmitted to structures controlling cognitive effort expenditure in order for it to manifest as behavior. We do not make a specific claim about the identity of this circuit, but the evidence presented in the review above, combined with the explanatory power of the model presented in

this paper, strongly suggest that it exists.

In conclusion, by viewing the allocation of metabolic resources as a control problem with the concrete resource limitation given by the dynamics of glycogen storage and use, we provide a family of novel explanations for a number of apparently unrelated phenomena while simultaneously providing a rational explanation for a range of biases and patterns in decision making. These new hypotheses are quantitative, testable, and we hope will provide grist for the development of new explanations and interventions.

Chapter 7

Conclusion

Performing a task requires information to be transmitted from the world, through the brain, and back into the world via action. The speed and fidelity of this transmission process is constrained by the presence of noise, the availability of energy, and the efficiency of inference afforded by knowledge of task statistics. In this dissertation, we have shown that a transmission process bounded by these constraints provides a parsimonious and simple explanation of a wide array of behavioral phenomena, including reproducing known 'laws' of human behavior such as the Hick-Hyman law and the Power Law of Practice.

In order to quantify the relationship between transmission constraints and measurable behavior, we introduced an information transmission scheme called the Bayes-Poisson model, which is constructed using stochastic processes, Bayesian inference, and entropy. In this model, the burden of increasing transmission efficiency is placed on the decoder, which can increase efficiency by capturing the task statistics in a decoder prior. In addition, the model provides a principled method of quantifying transmission costs associated with performing tasks. We have argued that it is exactly the set of tasks that require high transmission costs that produce the feeling of mental effort, and that effort may be a phenomenological signal to preserve signal transmission resources.

Finally, we used the Bayes-Poisson model to understand the process of information integration in the N-back task. By modifying the task to explicitly include statistical structure in the pattern of responses, we demonstrated that subjects produce responses by integrating information from multiple sources, augmenting traditional interpretations

of N-back performance and suggesting a deep similarity between the N-back task and cognitive control tasks.

Cognitive science is in need of both principles and parsimony. By acknowledging the role of and constraints on information transmission in the production of behavior in the service of a task, we have been able to produce simple and parsimonious explanations of a wide range of phenomena.

References

[1] Herbert A Simon. A behavioral model of rational choice. *The Quarterly Journal of Economics*, 69(1):99–118, 1955.

[2] William E Hick. On the rate of gain of information. *Quarterly Journal of Experimental Psychology*, 4(1):11–26, 1952.

[3] Ray Hyman. Stimulus information as a determinant of reaction time. *Journal of Experimental Psychology*, 45(3):188, 1953.

[4] Norbert Wiener. *Cybernetics Or Control and Communication in the Animal and the Machine*. MIT Press, 1965.

[5] Roy Lachman, Janet L Lachman, and Earl C Butterfield. *Cognitive psychology and information processing: An introduction*. Psychology Press, 1979.

[6] James V. Stone. *Principles of neural information theory: Computational neuroscience and metabolic efficiency*. Tutorial Introductions. Sebtel Press, 2018.

[7] David Marr. *Vision: A computational investigation into the human representation and processing of visual information*. Henry Holt and Co., Inc., New York, NY, USA, 1982.

[8] Barbara A Eriksen and Charles W Eriksen. Effects of noise letters upon the identification of a target letter in a nonsearch task. *Perception & Psychophysics*, 16(1):143–149, 1974.

[9] Colin M MacLeod. Half a century of research on the stroop effect: An integrative review. *Psychological Bulletin*, 109(2):163, 1991.

[10] Wouter Kool and Matthew Botvinick. A labor/leisure tradeoff in cognitive control. *Journal of Experimental Psychology: General*, 143(1):131–141, 2014.

[11] Amitai Shenhav, Matthew M Botvinick, and Jonathan D Cohen. The expected value of control: An integrative theory of anterior cingulate cortex function. *Neuron*, 79(2):217–240, 2013.

[12] Robert Kurzban, Angela Duckworth, Joseph W Kable, and Justus Myers. An opportunity cost model of subjective effort and task performance. *Behavioral and Brain Sciences*, 36(6):661–679, 2013.

[13] Claude Elwood Shannon. A mathematical theory of communication. *Bell System Technical Journal*, 27(3):379–423, 1948.

[14] Donald Laming. Statistical information and uncertainty: A critique of applications in experimental psychology. *Entropy*, 12(4):720–771, 2010.

[15] R Duncan Luce. Whatever happened to information theory in psychology? *Review of General Psychology*, 7(2):183, 2003.

[16] Fred Rieke, David Warland, Rob de Ruyter van Steveninck, and William Bialek. *Spikes: Exploring the neural code*. A Bradford Book, 1999.

[17] Ray Hyman. Stimulus information as a determinant of reaction time. *Journal of Experimental Psychology*, 45(3):188, 1953.

[18] Allen Newell and Paul S Rosenbloom. Mechanisms of skill acquisition and the law of practice. *Cognitive Skills and their Acquisition*, 1(1981):1–55, 1981.

[19] James V Stone. *Information theory: A tutorial introduction*. Sebtel Press, 2015.

[20] Thomas M Cover and Joy A Thomas. *Elements of information theory*. John Wiley & Sons, 2012.

[21] Abraham Wald. Sequential tests of statistical hypotheses. *The Annals of Mathematical Statistics*, 16(2):117–186, 1945.

[22] Roger Ratcliff, Philip L Smith, Scott D Brown, and Gail McKoon. Diffusion decision model: Current issues and history. *Trends in Cognitive Sciences*, 20(4):260–281, 2016.

[23] Richard P Heitz. The speed-accuracy tradeoff: History, physiology, methodology, and behavior. *Frontiers in Neuroscience*, 8:150, 2014.

[24] Sanjay G Manohar, Trevor T-J Chong, Matthew AJ Apps, Amit Batla, Maria Stamelou, Paul R Jarman, Kailash P Bhatia, and Masud Husain. Reward pays the cost of noise reduction in motor and cognitive control. *Current Biology*, 25(13):1707–1716, 2015.

[25] Il Memming Park and Jonathan W Pillow. Bayesian efficient coding. *bioRxiv*, page 178418, 2017.

[26] Richard M Shiffrin and Walter Schneider. Controlled and automatic human information processing: Ii. perceptual learning, automatic attending and a general theory. *Psychological Review*, 84(2):127, 1977.

[27] Robert A Jacobs and John K Kruschke. Bayesian learning theory applied to human cognition. *Wiley Interdisciplinary Reviews: Cognitive Science*, 2(1):8–21, 2011.

[28] John R Anderson, Michael Matessa, and Christian Lebiere. Act-r: A theory of higher level cognition and its relation to visual attention. *Human-Computer Interaction*, 12(4):439–462, 1997.

[29] Gordon D Logan. Toward an instance theory of automatization. *Psychological Review*, 95(4):492, 1988.

[30] Gordon D Logan. Shapes of reaction-time distributions and shapes of learning curves: A test of the instance theory of automaticity. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 18(5):883, 1992.

[31] George A Miller. The magical number seven, plus or minus two: Some limits on our capacity for processing information. *Psychological Review*, 63(2):81, 1956.

[32] Paul Rosenbloom and Allen Newell. Learning by chunking: A production system model of practice. *Production System Models of Learning and Development*, pages 221–286, 1987.

[33] Horace B Barlow. Possible principles underlying the transformations of sensory messages. *Sensory Communication, Contributions*, 1959.

[34] Simon Laughlin. A simple coding procedure enhances a neuron's information capacity. *Zeitschrift für Naturforschung C*, 36(9-10):910–912, 1981.

[35] William E Vinje and Jack L Gallant. Sparse coding and decorrelation in primary visual cortex during natural vision. *Science*, 287(5456):1273–1276, 2000.

[36] Xaq Pitkow and Markus Meister. Decorrelation and efficient coding by retinal ganglion cells. *Nature Neuroscience*, 15(4):628, 2012.

[37] Eero P Simoncelli and Bruno A Olshausen. Natural image statistics and neural representation. *Annual Review of Neuroscience*, 24(1):1193–1216, 2001.

[38] Robert Seibel. Discrimination reaction time for a 1,023-alternative task. *Journal of Experimental Psychology*, 66(3):215, 1963.

[39] Andrew Heathcote, Scott Brown, and DJK Mewhort. The power law repealed: The case for an exponential law of practice. *Psychonomic bulletin & review*, 7(2):185–207, 2000.

[40] Amos Tversky and Daniel Kahneman. Judgment under uncertainty: Heuristics and biases. *Science*, 185(4157):1124–1131, 1974.

[41] Falk Lieder, Thomas L Griffiths, Quentin JM Huys, and Noah D Goodman. The anchoring bias reflects rational use of cognitive resources. *Psychonomic Bulletin & Review*, 25(1):322–349, 2018.

[42] Adrienne L Fairhall, Geoffrey D Lewen, William Bialek, and Robert R de Ruyter van Steveninck. Efficiency and ambiguity in an adaptive neural code. *Nature*, 412(6849):787, 2001.

[43] Naama Brenner, William Bialek, and Rob de Ruyter Van Steveninck. Adaptive rescaling maximizes information transmission. *Neuron*, 26(3):695–702, 2000.

[44] Amitai Shenhav, Sebastian Musslick, Falk Lieder, Wouter Kool, Thomas L Griffiths, Jonathan D Cohen, and Matthew M Botvinick. Toward a rational and mechanistic account of mental effort. *Annual Review of Neuroscience*, 40:99–124, 2017.

[45] Michael J Kane, Andrew RA Conway, Timothy K Miura, and Gregory JH Colflesh. Working memory, attention control, and the n-back task: A question of construct validity. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 33(3):615, 2007.

[46] Susanne M Jaeggi, Martin Buschkuehl, Walter J Perrig, and Beat Meier. The concurrent validity of the n-back task as a working memory measure. *Memory*, 18(4):394–412, 2010.

[47] Jason Ralph. *Statistical manipulation and control strategies of the n-back task.* PhD thesis, Rensselaer Polytechnic Institute, Troy, NY, 2014.

[48] Wayne K Kirchner. Age differences in short-term retention of rapidly changing information. *Journal of Experimental Psychology*, 55(4):352, 1958.

[49] Jane F Mackworth. Paced memorizing in a continuous task. *Journal of Experimental Psychology*, 58(3):206, 1959.

[50] Michael J Kane and Randall W Engle. The role of prefrontal cortex in working-memory capacity, executive attention, and general fluid intelligence: An individual-differences perspective. *Psychonomic Bulletin & Review*, 9(4):637–671, 2002.

[51] Adrian M Owen, Kathryn M McMillan, Angela R Laird, and Ed Bullmore. Nback working memory paradigm: A metaanalysis of normative functional neuroimaging studies. *Human Brain Mapping*, 25(1):46–59, 2005.

[52] Andrew RA Conway, Michael J Kane, and Randall W Engle. Working memory capacity and its relation to general intelligence. *Trends in Cognitive Sciences*, 7(12):547–552, 2003.

[53] Klaus Oberauer. Binding and inhibition in working memory: Individual and age differences in short-term recognition. *Journal of Experimental Psychology: General*, 134(3):368, 2005.

[54] Jill T Shelton, Emily M Elliott, BD Hill, Matthew R Calamia, and Wm Drew Gouvier. A comparison of laboratory and clinical working memory tests and their prediction of fluid intelligence. *Intelligence*, 37(3):283–293, 2009.

[55] Rose Roberts and Edward Gibson. Individual differences in sentence memory. *Journal of Psycholinguistic Research*, 31(6):573–598, 2002.

[56] KM Miller, CC Price, MS Okun, H Montijo, and D Bowers. Is the n-back task a valid neuropsychological measure for assessing working memory. *Archives of Clinical Neuropsychology*, 24(7):711–717, 2009.

[57] Kristina T Ciesielski, Paul G Lesnik, Robert L Savoy, Ellen P Grant, and Seppo P Ahlfors. Developmental neural networks in children performing a categorical n-back task. *Neuroimage*, 33(3):980–990, 2006.

[58] MM Botvinick and JD Cohen. The computational and neural basis of cognitive control: Charted territory and new frontiers. *Cogn Sci*, 38(6):1249–1285, 2014.

[59] Matthew Botvinick and Todd Braver. Motivation and cognitive control: From behavior to neural mechanism. *Annual Review of Psychology*, 66:83–113, 2015.

[60] Jonathan D Cohen. Cognitive control: Core constructs and current considerations. *The Wiley handbook of cognitive control*, pages 1–28, 2017.

[61] David M Condon and William Revelle. The international cognitive ability resource: Development and initial validation of a public-domain measure. *Intelligence*, 43:52–64, 2014.

[62] Kevin Crowston. Amazon mechanical turk: A research tool for organizations and information systems scholars. In *Shaping the future of ICT research*, pages 210–221. Springer, 2012.

[63] Daniel Kersten, Pascal Mamassian, and Alan Yuille. Object perception as bayesian inference. *Annual Review Psychology*, 55:271–304, 2004.

[64] Konrad P Kording and Daniel M Wolpert. Bayesian integration in sensorimotor learning. *Nature*, 427(6971):244, 2004.

[65] Andrew Westbrook, Daria Kester, and Todd S Braver. What is the subjective cost of cognitive effort? load, trait, and aging effects revealed by economic preference. *PLoS One*, 8(7):e68210, 2013.

[66] Gerd Gigerenzer and Daniel G Goldstein. Reasoning the fast and frugal way: Models of bounded rationality. *Psychological Review*, 103(4):650, 1996.

[67] Michael Balle. La loi du moindre effort mental: Les representations mentales. *Sciences humaines*, (128):36–39, 2002.

[68] Susan T Fiske and Shelley E Taylor. *Social cognition*. Mcgraw-Hill Book Company, 1991.

[69] G Dreisbach and R Fischer. Conflicts as aversive signals. *Brain Cogn*, 78(2):94–98, 2012.

[70] Robert P Spunt, Matthew D Lieberman, Jessica R Cohen, and Naomi I Eisenberger. The phenomenology of error processing: The dorsal acc response to stop-signal errors tracks reports of negative affect. *Journal of Cognitive Neuroscience*, 24(8):1753–1765, 2012.

[71] Joseph T McGuire and Matthew M Botvinick. Prefrontal cortex, cognitive control, and the registration of decision costs. *Proceedings of the National Academy of Sciences of the USA*, 107(17):7922–7926, 2010.

[72] James M Gold, Wouter Kool, Matthew M Botvinick, Leeka Hubzin, Sharon August, and James A Waltz. Cognitive effort avoidance and detection in people with

schizophrenia. *Cognitive, Affective, & Behavioral Neuroscience*, 15(1):145–154, 2015.

[73] Wouter Kool, Joseph T McGuire, Zev B Rosen, and Matthew M Botvinick. Decision making and the avoidance of cognitive demand. *Journal of Experimental Psychology: General*, 139(4):665–682, 2010.

[74] Margaret Lynn, Travis A. Riddle, and Ezequiel Morsella. The phenomenology of quitting: Effects from repetition and cognitive effort. *Korean Journal of Cognitive Science*, 23:25–46, 2012.

[75] Alice F Healy, James A Kole, Carolyn J Buck-Gengle, and Lyle E Bourne. Effects of prolonged work on data entry speed and accuracy. *Journal of Experimental Psychology: Applied*, 10(3):188–199, 2004.

[76] Bastien Blain, Guillaume Hollard, and Mathias Pessiglione. Neural mechanisms underlying the impact of daylong cognitive work on economic decisions. *Proceedings of the National Academy of Sciences of the USA*, 113(25):6967–6972, 2016.

[77] Masaaki Tanaka, Akira Ishii, and Yasuyoshi Watanabe. Neural effects of mental fatigue caused by continuous attention load: A magnetoencephalography study. *Brain Research*, 1561:60–66, 2014.

[78] John A Bargh. The four horsemen of automaticity: Awareness, intention, efficiency, and control in social cognition. *Handbook of Social Cognition*, 1:1–40, 1994.

[79] Nathaniel D Daw, Yael Niv, and Peter Dayan. Uncertainty-based competition between prefrontal and dorsolateral striatal systems for behavioral control. *Nature Neuroscience*, 8(12):1704, 2005.

[80] George S Snoddy. Learning and stability: A psychophysiological analysis of a case of motor learning with clinical applications. *Journal of Applied Psychology*, 10(1):1, 1926.

[81] John R Anderson, Daniel Bothell, Michael D Byrne, Scott Douglass, Christian Lebiere, and Yulin Qin. An integrated theory of the mind. *Psychological Review*, 111(4):1036, 2004.

[82] Joel S Warm, Raja Parasuraman, and Gerald Matthews. Vigilance requires hard mental work and is stressful. *Human Factors*, 50(3):433–441, 2008.

[83] Andy Clark. *Supersizing the mind: Embodiment, action, and cognitive extension*. OUP USA, 2008.

[84] Anthony Chemero. *Radical embodied cognitive science*. MIT press, 2011.

[85] JA Droll and MM Hayhoe. Trade-offs between gaze and working memory use. *Journal of Experimental Psychology: Human Perception and Performance*, 33(6):1352–1365, 2007.

[86] Colin M MacLeod. The stroop task: The "gold standard" of attentional measures. *Journal of Experimental Psychology: General*, 121(1):12, 1992.

[87] *Fatigue of cognitive control in the stroop-task*, volume 31, 2009.

[88] Gesine Dreisbach and Rico Fischer. Conflicts as aversive signals for control adaptation. *Current Directions in Psychological Science*, 24(4):255–260, 2015.

[89] Frederick Verbruggen and Gordon D Logan. Response inhibition in the stop-signal paradigm. *Trends in Cognitive Sciences*, 12(11):418–424, 2008.

[90] Keith E Stanovich. *The robots rebellion: Finding meaning in the age of Darwin*. University of Chicago Press, 2005.

[91] Tobias Egner. *The Wiley handbook of cognitive control*. John Wiley & Sons, 2017.

[92] Adele Diamond. Executive functions. *Annual review of psychology*, 64:135–168, 2013.

[93] David A Grant and Esta Berg. A behavioral analysis of degree of reinforcement and ease of shifting to new responses in a weigl-type card-sorting problem. *Journal of Experimental Psychology*, 38(4):404, 1948.

[94] Matthew L Dixon and Kalina Christoff. The decision to engage cognitive control is driven by expected reward-value: Neural and behavioral evidence. *PLoS One*, 7(12):e51637, 2012.

[95] Robert Rosenman, Vidhura Tennekoon, and Laura G Hill. Measuring bias in self-reported data. *International Journal of Behavioural and Healthcare Research*, 2(4):320–332, 2011.

[96] Russell H Fazio, David M Sanbonmatsu, Martha C Powell, and Frank R Kardes. On the automatic activation of attitudes. *Journal of Personality and Social Psychology*, 50(2):229–238, 1986.

[97] David R Herring, Katherine R White, Linsa N Jabeen, Michelle Hinojos, Gabriela Terrazas, Stephanie M Reyes, Jennifer H Taylor, and Stephen L Crites. On the automatic activation of attitudes: A quarter century of evaluative priming research. *Psychological Bulletin*, 139(5):1062–1089, 2013.

[98] Timothy L Dunn, David J C Lutes, and Evan F Risko. Metacognitive evaluation in the avoidance of demand. *J Exp Psychol Hum Percept Perform*, 42(9):1372–1387, 2016.

[99] Martin S Hagger, Chantelle Wood, Chris Stiff, and Nikos L Chatzisarantis. Ego depletion and the strength model of self-control: A meta-analysis. *Psychological Bulletin*, 136(4):495–525, 2010.

[100] Tsuru Arai. *Mental fatigue*, volume (54). Teachers College, Columbia University, 1912.

[101] Zelma L Huxtable, Miriam H White, and Marjorie A McCartor. A re-performance and re-interpretation of the arai experiment in mental fatigue with three subjects. *Psychological Monographs*, 59(5):i, 1945.

[102] Martin S Hagger, Nikos LD Chatzisarantis, Hugo Alberts, Calvin O Anggono, Cedric Batailler, Angela R Birt, Ralf Brand, Mark J Brandt, Gene Brewer, and Sabrina Bruyneel. A multilab preregistered replication of the ego-depletion effect. *Perspectives on Psychological Science*, 11(4):546–573, 2016.

[103] John L. Andreassi. *Psychophysiology.* Psychology Press, 2010.

[104] Robert B Layzer. Muscle metabolism during fatigue and work. *Bailliere's Clinical Endocrinology and Metabolism*, 4(3):441–459, 1990.

[105] Dieter Leyk, Uwe Hoffmann, Klaus Baum, and D Essfeld. Time courses of cardiac output and oxygen uptake following stepwise increases in exercise intensity. *International Journal of Sports Medicine*, 16(6):357–363, 1995.

[106] Amitai Shenhav, Sebastian Musslick, Falk Lieder, Wouter Kool, Thomas L Griffiths, Jonathan D Cohen, and Matthew M Botvinick. Toward a rational and mechanistic account of mental effort. *Annual Review of Neuroscience*, 40:99–124, 2017.

[107] David Navon and Daniel Gopher. On the economy of the human-processing system. *Psychological Review*, 86(3):214, 1979.

[108] Gordon D Logan. Skill and automaticity: Relations, implications, and future directions. *Canadian Journal of Psychology*, 39(2):367, 1985.

[109] Walter Schneider and Richard M Shiffrin. Controlled and automatic human information processing: I. detection, search, and attention. *Psychological Review*, 84(1):1, 1977.

[110] Michael Inzlicht, Brandon J Schmeichel, and C Neil Macrae. Why self-control seems (but may not be) limited. *Trends in Cognitive Sciences*, 18(3):127–133, 2014.

[111] Stephen H Fairclough and Kim Houston. A metabolic measure of mental effort. *Biological Psychology*, 66(2):177–190, 2004.

[112] Jolene Feldman and Immanuel Barshi. The effects of blood glucose levels on cognitive performance: A review of the literature. *National Aeronautics and Space Administration*, 2007.

[113] Roy F Baumeister, Dianne M Tice, and Kathleen D Vohs. The strength model of self-regulation: Conclusions from the second decade of willpower research. *Perspectives on Psychological Science*, 2018.

[114] Matthew T Gailliot, Roy F Baumeister, C Nathan DeWall, Jon K Maner, E Ashby Plant, Dianne M Tice, Lauren E Brewer, and Brandon J Schmeichel. Self-control relies on glucose as a limited energy source: Willpower is more than a metaphor. *Journal of Personality and Social Psychology*, 92(2):325, 2007.

[115] Michael Inzlicht and Brandon J Schmeichel. What is ego depletion? toward a mechanistic revision of the resource model of self-control. *Perspectives on Psychological Science*, 7(5):450–463, 2012.

[116] David Benton and Deborah S Owens. Blood glucose and human memory. *Psychopharmacology*, 113(1):83–88, 1993.

[117] Suzanne Craft, Christopher Murphy, and Jennifer Wemstrom. Glucose effects on complex memory and nonmemory tasks: The influence of age, sex, and glucoregulatory response. *Psychobiology*, 22(2):95–105, 1994.

[118] Clarissa Smith Holmes, John T Hayford, Jose L Gonzalez, and Joy A Weydert. A survey of cognitive functioning at different glucose levels in diabetic persons. *Diabetes Care*, 6(2):180–185, 1983.

[119] John D Blackman, Vernon L Towle, Gary F Lewis, Jean-Paul Spire, and Kenneth S Polonsky. Hypoglycemic thresholds for cognitive dysfunction in humans. *Diabetes*, 39(7):828–835, 1990.

[120] Mark L Evans, Andrew Pernet, Jill Lomas, Jenny Jones, and Stephanie A Amiel. Delay in onset of awareness of acute hypoglycemia and of restoration of cognitive performance during recovery. *Diabetes Care*, 23(7):893–897, 2000.

[121] Clarissa S Holmes, Kathleen M Koepke, and Robert G Thompson. Simple versus complex performance impairments at three blood glucose levels. *Psychoneuroendocrinology*, 11(3):353–357, 1986.

[122] Rachael T Donohoe and David Benton. Declining blood glucose levels after a cognitively demanding task predict subsequent memory. *Nutritional Neuroscience*, 2(6):413–424, 1999.

[123] Michael W Parsons and Paul E Gold. Glucose enhancement of memory in elderly humans: An inverted-u dose-response curve. *Neurobiology of Aging*, 13(3):401–404, 1992.

[124] Donna L Korol and Paul E Gold. Glucose, memory, and aging. *The American Journal of Clinical Nutrition*, 67(4):764S–771S, 1998.

[125] MM Maassen, T Lingenfelser, H Gluck, W Renn, M Eggstein, and B Jakober. Cognitive and psychomotor function during hypoglycemia: A comparison between porcine and human insulin. *Neuropsychobiology*, 24(1):30–36, 1990.

[126] Anthony B Stevens, William R McKane, Patrick M Bell, Paul Bell, David J King, and John R Hayes. Psychomotor performance and counterregulatory responses during mild hypoglycemia in healthy volunteers. *Diabetes Care*, 12(1):12–17, 1989.

[127] A Westbrook and TS Braver. Cognitive effort: A neuroeconomic approach. *Cognitive, Affective, & Behavioral Neuroscience*, 15(2):395–415, 2015.

[128] Wouter Kool and Matthew Botvinick. Mental labour. *Nature Human Behaviour*, page 1, 2018.

[129] Alexander Thiele and Mark A Bellgrove. Neuromodulation of attention. *Neuron*, 97(4):769–785, 2018.

[130] Robert Desimone and John Duncan. Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18(1):193–222, 1995.

[131] Daniel Kahneman. *Attention and effort*. Prentice-Hall, 1973.

[132] Norman H Mackworth. The breakdown of vigilance during prolonged visual search. *Quarterly Journal of Experimental Psychology*, 1:6–21, 1948.

[133] Lionel Naccache, Stanislas Dehaene, Laurent Cohen, Marie-Odile Habert, Elodie Guichart-Gomez, Damien Galanaud, and Jean-Claude Willer. Effortless control: Executive attention and conscious feeling of mental effort are dissociable. *Neuropsychologia*, 43(9):1318–1328, 2005.

[134] Jan Drugowitsch, Rubn Moreno-Bote, Anne K Churchland, Michael N Shadlen, and Alexandre Pouget. The cost of accumulating evidence in perceptual decision making. *Journal of Neuroscience*, 32(11):3612–3628, 2012.

[135] Yaffa Yeshurun and Einat Rashal. Precueing attention to the target location diminishes crowding and reduces the critical distance. *Journal of Vision*, 10:16, 2010.

[136] Jerome Prado, Joshua Carp, and Daniel H Weissman. Variations of response time in a selective attention task are linked to variations of functional connectivity in the attentional network. *Neuroimage*, 54(1):541–549, 2011.

[137] John HR Maunsell and Stefan Treue. Feature-based attention in visual cortex. *Trends in Neurosciences*, 29(6):317–322, 2006.

[138] Miranda Scolari and John T Serences. Adaptive allocation of attentional gain. *Journal of Neuroscience*, 29(38):11933–11942, 2009.

[139] WJ Ma, M Husain, and PM Bays. Changing concepts of working memory. *Nature Neuroscience*, 17(3):347–356, 2014.

[140] Alison M Gilbert and Julie A Fiez. Integrating rewards and cognition in the frontal cortex. *Cognitive, Affective, & Behavioral Neuroscience*, 4:540–552, 2004.

[141] Richard P Heitz, Josef C Schrock, Tabitha W Payne, and Randall W Engle. Effects of incentive on working memory capacity: Behavioral and pupillometric data. *Psychophysiology*, 45(1):119–129, 2008.

[142] Richard C Atkinson and Richard M Shiffrin. Human memory: A proposed system and its control processes. In *Psychology of learning and motivation*, volume 2, pages 89–195. Academic Press, 1968.

[143] Ronald Van den Berg, Hongsup Shin, Wen-Chuang Chou, Ryan George, and Wei Ji Ma. Variability in encoding precision accounts for visual short-term memory limitations. *Proceedings of the National Academy of Sciences*, 109(22):8780–8785, 2012.

[144] John R Anderson. *Cognitive psychology and its implications*. Macmillan, 2005.

[145] Ellen J Langer, Arthur Blank, and Benzion Chanowitz. The mindlessness of ostensibly thoughtful action: The role of. "placebic" information in interpersonal interaction. *Journal of Personality and Social Psychology*, 36(6):635, 1978.

[146] K Anders Ericsson, Ralf T Krampe, and Clemens Tesch-Romer. The role of deliberate practice in the acquisition of expert performance. *Psychological Review*, 100(3):363, 1993.

[147] T Drew, ML V, and JM Wolfe. The invisible gorilla strikes again: Sustained inattentional blindness in expert observers. *Psychological Science*, 24(9):1848–1853, 2013.

[148] Daniel J Simons and Christopher F Chabris. Gorillas in our midst: Sustained inattentional blindness for dynamic events. *Perception*, 28(9):1059–1074, 1999.

[149] Terezinha Nunes Carraher, David William Carraher, and Analucia Dias Schliemann. Mathematics in the streets and in schools. *British journal of developmental psychology*, 3(1):21–29, 1985.

[150] Randall C OReilly, Seth A Herd, and Wolfgang M Pauli. Computational models of cognitive control. *Current Opinion in Neurobiology*, 20(2):257–261, 2010.

[151] Gabriele Gratton, Michael GH Coles, and Emanuel Donchin. Optimizing the use of information: Strategic control of activation of responses. *Journal of Experimental Psychology: General*, 121(4):480, 1992.

[152] MM Botvinick. Conflict monitoring and decision making: Reconciling two perspectives on anterior cingulate function. *Cognitive, Affective, & Behavioral Neuroscience*, 7(4):356–366, 2007.

[153] Douglas J Mewhort, Jacqueline G Braun, and Andrew Heathcote. Response time distributions and the stroop task: A test of the cohen, dunbar, and mcclelland (1990) model. *Journal of Experimental Psychology: Human Perception and Performance*, 18(3):872, 1992.

[154] Stephen Monsell. Task switching. *Trends in Cognitive Sciences*, 7(3):134–140, 2003.

[155] Monicque M Lorist, Merel Klein, Sander Nieuwenhuis, Ritske De Jong, Gijsbertus Mulder, and Theo F Meijman. Mental fatigue and task control: Planning and preparation. *Psychophysiology*, 37(5):614–625, 2000.

[156] Herbert A Simon. A study of decision-making processes in administrative organizations. *Administrative Behavior*, 1957.

[157] Thomas L Griffiths, Falk Lieder, and Noah D Goodman. Rational use of cognitive resources: Levels of analysis between the computational and the algorithmic. *Topics in Cognitive Science*, 7(2):217–229, 2015.

[158] Daniel Kahneman and Patrick Egan. *Thinking, fast and slow*, volume 1. Farrar, Straus and Giroux New York, 2011.

[159] Peter W Battaglia, Jessica B Hamrick, and Joshua B Tenenbaum. Simulation as an engine of physical scene understanding. In *Proceedings of the National Academy of Science*, volume 110, pages 18327–18332, 2013.

[160] Scott Thomas Christie and Paul Schrater. Cognitive cost as dynamic allocation of energetic resources. *Frontiers in Neuroscience*, 9:289, 2015.

[161] A. David Redish. *The mind within the brain: How we make decisions and how those decisions go wrong.* Oxford University Press, 2013.

[162] William J. McGuire. The nature of attitudes and attitude change. *The Handbook of Social Psychology*, 3:136–314, 1969.

[163] Shelley E Taylor. The interface of cognitive and social psychology. *Cognition, Social Behavior, and the Environment*, pages 189–211, 1981.

[164] Wouter Kool and Matthew Botvinick. A labor/leisure tradeoff in cognitive control. *Journal of Experimental Psychology: General*, 12 2012.

[165] Richard L. Solomon. The influence of work on behavior. *Psychological Bulletin*, 45(1):1, 1948.

[166] Colin F. Camerer and Robin M. Hogarth. The effects of financial incentives in experiments: A review and capital-labor-production framework. *Journal of Risk and Uncertainty*, 19(1-3):7–42, 1999.

[167] Koji Jimura, Hannah S. Locke, and Todd S. Braver. Prefrontal cortex mediation of cognitive enhancement in rewarding motivational contexts. *Proceedings of the National Academy of Sciences*, 107(19):8871–8876, 5 2010.

[168] Ruth M Krebs, Carsten N Boehler, and Marty G Woldorff. The influence of reward associations on conflict processing in the stroop task. *Cognition*, 117(3):341–347, 2010.

[169] Evan C. Carter and Michael E. McCullough. Publication bias and the limited strength model of self-control: Has the evidence for ego depletion been overestimated? *Frontiers in Psychology*, 5:823, 2014.

[170] Pearl Y Martin and David Benton. The influence of a glucose drink on a demanding working memory task. *Physiology & Behavior*, 67(1):69–74, 8 1999.

[171] David Benton and Pearl Y. Parker. Breakfast, blood glucose, and cognition. *The American Journal of Clinical Nutrition*, 67(4):772S–778S, 1998.

[172] David O Kennedy and Andrew B Scholey. Glucose administration, heart rate and cognitive performance: Effects of increasing mental effort. *Psychopharmacology*, 149(1):63–71, 3 2000.

[173] David Benton and Julia Sargent. Breakfast, blood glucose and memory. *Biological Psychology*, 33(2-3):207–210, 7 1992.

[174] Mark L Evans, Andrew Pernet, Jill Lomas, Jenny Jones, and Stephanie A Amiel. Delay in onset of awareness of acute hypoglycemia and of restoration of cognitive performance during recovery. *Diabetes Care*, 23(7):893–7, 7 2000.

[175] Ann E Gold, Kenneth M MacLeod, Ian J Deary, and Brian M Frier. Hypoglycemia-induced cognitive dysfunction in diabetes mellitus: Effect of hypoglycemia unawareness. *Physiology & Behavior*, 58(3):501–11, 9 1995.

[176] Hartmut Schächinger, Daniel Cox, Lilly Linder, Stuart Brody, and Ulrich Keller. Cognitive and psychomotor function in hypoglycemia: Response error patterns and retest reliability. *Pharmacology Biochemistry and Behavior*, 75(4):915–20, 7 2003.

[177] Daniel J Cox, Linda Gonder-Frederick, and William Clarke. Driving decrements in type i diabetes during moderate hypoglycemia. *Diabetes*, 42(2):239–43, 2 1993.

[178] S. Pramming, B. Thorsteinsson, A. Theilgaard, E. M. Pinner, and C. Binder. Cognitive function during hypoglycaemia in type i diabetes mellitus. *British Medical Journal (Clinical Research Edition)*, 292(6521):647–50, 3 1986.

[179] Clarissa Smith Holmes, John T. Hayford, Jose L. Gonzalez, and Joy A. Weydert. A survey of cognitive functioning at different glucose levels in diabetic persons. *Diabetes Care*, 6(2):180–185, 3 1983.

[180] Richard G Hoffman, Diana J Speelman, Deborah A Hinnen, Kirby L Conley, Richard A Guthrie, and Robert K Knapp. Changes in cortical functioning with acute hypoglycemia and hyperglycemia in type i diabetes. *Diabetes Care*, 12(3):193–7, 3 1989.

[181] Rory J McCrimmon, Ian J Deary, and Brian M Frier. Auditory information processing during acute insulin-induced hypoglycaemia in non-diabetic human subjects. *Neuropsychologia*, 35(12):1547–53, 12 1997.

[182] Vincent McAulay, Ian J Deary, Stewart C Ferguson, and Brian M Frier. Acute hypoglycemia in humans causes attentional dysfunction while nonverbal intelligence is preserved. *Diabetes Care*, 24(10):1745–50, 10 2001.

[183] Ralf Lobmann, Henderikus G Smid, Gesine Pottag, Katrin Wagner, Hans-Joachim Heinze, and Hendrik Lehnert. Impairment and recovery of elementary cognitive function induced by hypoglycemia in type-1 diabetic patients and healthy controls. *The Journal of Clinical Endocrinology & Metabolism*, 85(8):2758–66, 8 2000.

[184] Daniel J Cox, Linda A Gonder-Frederick, Boris P Kovatchev, Diana M Julian, and William L Clarke. Progressive hypoglycemia's impact on driving simulation

performance. occurrence, awareness and correction. *Diabetes Care*, 23(2):163–70, 2 2000.

[185] Clarissa S Holmes, Kathleen M Koepke, and Robert G Thompson. Simple versus complex performance impairments at three blood glucose levels. *Psychoneuroendocrinology*, 11(3):353–7, 1986.

[186] Carol A Manning, JL Hall, and Paul Ernest Gold. Glucose effects on memory and other neuropsychological tests in elderly humans. *Psychological Science*, 1(5):307–311, 1990.

[187] David Benton and Deborah S. Owens. Blood glucose and human memory. *Psychopharmacology*, 113(1):83–88, 11 1993.

[188] Suzanne Craft, Christopher Murphy, and Jennifer Wemstrom. Glucose effects on complex memory and nonmemory tasks: The influence of age, sex, and glucoregulatory response. *Psychobiology*, 22(2):95–105, 6 1994.

[189] Rachael T Donohoe and David Benton. Cognitive functioning is susceptible to the level of blood glucose. *Psychopharmacology*, 145(4):378–385, 1999.

[190] Andrew B Scholey, Susan Harper, and David O Kennedy. Cognitive demand and blood glucose. *Physiology & Behavior*, 73(4):585–92, 7 2001.

[191] Alice F. Healy, James A. Kole, Carolyn J. Buck-Gengle, and Lyle E. Bourne. Effects of prolonged work on data entry speed and accuracy. *Journal of Experimental Psychology: Applied*, 10(3):188–99, 9 2004.

[192] M. M. Lorist, M. Klein, S. Nieuwenhuis, R. De Jong, G. Mulder, and T. F. Meijman. Lorist, monicque m and klein, merel and nieuwenhuis, sander and de jong, ritske and mulder, gijsbertus and meijman, theo f. *Psychophysiology*, 37(5):614–25, 9 2000.

[193] Matthew T. Gailliot, Roy F. Baumeister, C. Nathan DeWall, Jon K. Maner, E. Ashby Plant, Dianne M. Tice, Lauren E. Brewer, and Brandon J. Schmeichel. Self-control relies on glucose as a limited energy source: Willpower is more than a metaphor. *Journal of Personality and Social Psychology*, 92(2):325–36, 2 2007.

[194] Helen J Huang, Rodger Kram, and Alaa A Ahmed. Reduction of metabolic cost during motor learning of arm reaching dynamics. *Journal of Neuroscience*, 32(6):2182–2190, 2012.

[195] Joel Benington. Restoration of brain energy metabolism as the function of sleep. *Progress in Neurobiology*, 45(4):347–360, 3 1995.

[196] Rolf Gruetter. In vivo 13c nmr studies of compartmentalized cerebral carbohydrate metabolism. *Neurochemistry International*, 41(2-3):143–154, 8 2002.

[197] Matthew T. Gailliot. Unlocking the energy dynamics of executive functioning: Linking executive functioning to brain glycogen. *Perspectives on Psychological Science*, 3(4):245–263, 2008.

[198] Angus M. Brown. Brain glycogen re-awakened. *Journal of Neurochemistry*, 89(3):537–552, 5 2004.

[199] Ian A. Simpson, Anthony Carruthers, and Susan J. Vannucci. Supply and demand in cerebral energy metabolism: The role of nutrient transporters. *Journal of Cerebral Blood Flow & Metabolism*, 27(11):1766–91, 11 2007.

[200] Angus M. Brown, Selva Baltan Tekkök, and Bruce R. Ransom. Glycogen regulation and functional role in mouse white matter. *The Journal of Physiology*, 549(Pt 2):501–12, 6 2003.

[201] In-Young Y. Choi, Elizabeth R. Seaquist, and Rolf Gruetter. Effect of hypoglycemia on brain glycogen metabolism in vivo. *Journal of Neuroscience Research*, 72(1):25–32, 4 2003.

[202] Raymond A. Swanson. Physiologic coupling of glial glycogen metabolism to neuronal activity in brain. *Canadian Journal of Psychology and Pharmacology*, 70 Suppl:S138–44, 1992.

[203] Raymond A. Swanson, Matthew M. Morton, Stephen M. Sagar, and Frank R. Sharp. Sensory stimulation induces local cerebral glycogenolysis: Demonstration by autoradiography. *Neuroscience*, 51(2):451–61, 11 1992.

[204] Gerald A. Dienel and Nancy F. Cruz. Astrocyte activation in working brain: Energy supplied by minor substrates. *Neurochemistry International*, 48(6-7):586–595, 5 2006.

[205] S. R. Nelson, D. W. Schulz, Janet V. Passonneau, and O. H. Lowry. Control of glycogen levels in the brain. *Journal of Neurochemistry*, 15(11):1271–1279, 11 1968.

[206] V. Karadzic and Bogomir Mrsulja. Deprivation of paradoxical sleep and brain glycogen. *Journal of Neurochemistry*, 16(1):29–34, 1 1969.

[207] Creighton H. Phelps. Barbiturate-induced glycogen accumulation in brain. an electron microscopic study. *Brain Research*, 39(1):225–234, 4 1972.

[208] Stephen M. Sagar, Frank R. Sharp, and Raymond A. Swanson. The regional distribution of glycogen in rat brain fixed by microwave irradiation. *Brain Research*, 417(1):172–4, 8 1987.

[209] Angus M. Brown and Bruce R. Ransom. Astrocyte glycogen and brain energy metabolism. *Glia*, 55(12):1263–71, 9 2007.

[210] V. W. Pentreath and M. A. Kai-Kai. Significance of the potassium signal from neurons to glial cells. *Nature*, 295(5844):59–61, 1 1982.

[211] Dwight E Bergles and Craig E Jahr. Synaptic activation of glutamate transporters in hippocampal astrocytes. *Neuron*, 19(6):1297–308, 12 1997.

[212] Robert G Shulman, Fahmeed Hyder, and Douglas L Rothman. Cerebral energetics and the glycogen shunt: Neurochemical basis of functional imaging. *Proceedings of the National Academy of Sciences of the USA*, 98(11):6417–22, 5 2001.

[213] Matthew Botvinick and Todd Braver. Motivation and cognitive control: From behavior to neural mechanism. *Annual Review of Psychology*, 66:83–113, 1 2015.

[214] Sander Nieuwenhuis and Nick Yeung. Neural mechanisms of attention and control: Losing our inhibitions? *Nature Neuroscience*, 8(12):1631–1633, 2005.

[215] Keith E Stanovich and Richard F West. Individual differences in reasoning: Implications for the rationality debate. *Behavioral and Brain Sciences*, 23(5):645–665, 2000.

[216] Jonathan St BT Evans. Dual-processing accounts of reasoning, judgment, and social cognition. *Annual Review of Psychology*, 59:255–278, 2008.

[217] Maarten A. S. Boksem, Theo F. Meijman, and Monicque M. Lorist. Mental fatigue, motivation and action monitoring. *Biological Psychology*, 72(2):123–32, 5 2006.

[218] Takashi Matsui, Shingo Soya, Masahiro Okamoto, Yukio Ichitani, Kentaro Kawanaka, and Hideaki Soya. Brain glycogen decreases during prolonged exercise. *The Journal of Physiology*, 589(13):3383–3393, 7 2011.

[219] Dimitri P. Bertsekas. *Dynamic programming and optimal control*. Athena Scientific, 2017.

[220] Yael Niv, Nathaniel D. Daw, and Peter Dayan. How fast to work: Response vigor, motivation and tonic dopamine. In *Neural Information Processing Systems*, volume 18, pages 1019–1026, 2005.

[221] Karl Friston, Francesco Rigoli, Dimitri Ognibene, Christoph Mathys, Thomas Fitzgerald, and Giovanni Pezzulo. Active inference and epistemic value. 2015.

[222] Daphne Bavelier, C. Shawn Green, Alexandre Pouget, and Paul Schrater. Brain plasticity through the life span: Learning to learn and action video games. *Annual Review of Neuroscience*, 35:391–416, 2012.